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Spatial and temporal modelling of insect pests and their host plants under climate change

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SUMMARY

Agriculture is facing the major challenge of providing food security for a growing human population without jeopardizing the environment. Meanwhile, climate change is putting additional pressure on crop production, as current challenges are amplified and new ones emerge. Besides the well-known direct impact of abiotic changes, such as increasing heat stress or changing precipitation regimes, a key question remains in how far biotic factors in form of insect pests will further undermine crop production under climate change. Insects, being ectotherms, are highly dependent on thermal changes and therefore directly respond to raising temperatures. Under warmer temperatures, local, already established insect pests are expected to exhibit more generations, faster population growth, and increasing metabolism and newly occurring, invasive insect pests may put additional pressure on agriculture. While globalisation supports species to overcome natural barriers, they find increasingly suitable conditions as climate warms. Therefore, the risk of insect pest invasion is increasing with climate change, particularly in higher latitudes, where cold winter temperatures have previously limited insect pest distributions. Preparing for increasing pest pressure and anticipating invasions of insect pest species to protect agricultural food production, will require a better understanding of potential shifts in insect pest distribution under climate change.

This thesis aimed at providing a better understanding of how the distribution of insect pests will respond to climate change. To tackle this question, I used different spatial modelling approaches to investigate the climatic niches of insect pest species and their host plants. Mapping those niches spatially provided information on the potential distribution ranges of insect pest species. The first chapter investigated potential range shifts of black-listed insect pest species and their host plants using correlative models. I evaluated the spatial and temporal dynamics of predicted future interactions between insect pests and their known host plants using a metaweb approach. The second chapter compared two complementary modelling approaches to examine differences between fundamental and realized climatic niches of insect pests and their distribution along temperature gradients. The third chapter used deep neural network algorithms to identify pest damages in the field and couples the occurrence of pest damages with meteorological data. This chapter served as a proof of concept study for the integration of new technologies into pest damage forecasting.

This thesis showed that climate change leads to shifts of potential distributions of insect pest species (*Chapter 1* and *Chapter 2*) and cultivated plants (*Chapter 1*) within Europe. In particular, *Chapter 1* used datasets of 89 black-listed insect pest species and 126 crops and forest tree species to show that southern European regions are under high pest pressure posed by non-native species already under current climate. Meanwhile, in northern European regions agriculture may benefit from improved climatic suitability for cultivated plants. However, at the same time, in these regions, yield may become more vulnerable to insect pests as the changing climate allows the survival of new pest species. *Chapter 2* compared physiological and correlative species distribution models, yielding good model agreement despite conceptual differences, therefore providing additional robustness to the inferences. With both modelling approaches, I identified a threshold of temperature beyond which the number of pest species with suitable climatic conditions will rapidly increase. Together, the results from *Chapter 1* and *Chapter 2* deliver strong arguments that new invasive insect pest species will enter Europe in the near future, underlining that there is a growing urge for development of new pest management strategies to cope with such invasions. *Chapter 3* showed how the combination of big data and deep learning may provide new solutions for pest damage forecasting, uncovering new opportunities for sustainable plant protection from exploiting innovative technologies.

Together, the three chapters of this thesis contribute to a better understanding of the impact of climate change on the distribution of insect pests and their host plants. In particular, this thesis combines comprehensive datasets of insect pests, agricultural crops and forest tree species in order to identify regions under elevated pest pressure and introduces a new method for pest forecasting. The chapters of this thesis provide a scientific basis for improvement of plant protection and pest management.

ZUSAMMENFASSUNG

Die Landwirtschaft steht der grossen Herausforderung gegenüber, die Ernährungssicherheit für eine wachsende Bevölkerung zu gewährleisten und gleichzeitig die unerwünschten Umweltwirkungen zu minimieren. Der Klimawandel übt zusätzlichen Druck auf den Pflanzenbau aus, indem gegenwärtige Herausforderungen verstärkt und gleichzeitig neue hervorgerufen werden. Neben den direkten Einflüssen von abiotischen Veränderungen, wie zum Beispiel erhöhtem Hitzestress und veränderten Niederschlagsmustern, die durch den Kimawandel hervorgerufen werden, eröffnet sich eine weitere Schlüsselfrage bezüglich des Einflusses von biotischen Faktoren, welche in Form von Schadinsekten den Pflanzenbau gefährden. Insekten sind als ektotherme Organismen stark von Veränderungen der Umgebungstemperatur abhängig und reagieren deshalb direkt auf den Klimawandel. Man muss davon ausgehen, dass mit den steigenden Temperaturen die lokalen, etablierten Schadinsekten eine erhöhte Anzahl Generationen aufweisen, die Populationen schneller wachsen, der Stoffwechsel erhöht wird, und neu auftretende, gebietsfremde Arten zusätzlichen Druck auf die Landwirtschaft ausüben. Die Globalisierung hilft Arten natürliche Grenzen zu überwinden und dadurch neue Gebiete zu besiedeln, in denen sie zunehmend geeignete klimatische Bedingungen vorfinden. Vor allem in höheren Breitengraden haben kalte Wintertemperaturen bis anhin die Verbreitung eingeschränkt, weshalb sich dort das Risiko durch neue invasive Arten erhöht. Eine bessere Kenntnis über die potentiellen Verschiebungen der Verbreitungsgebiete von Schadinsekten im Klimawandel trägt zur Vorbereitung auf den steigenden Schädlingsdruck bei und hilft somit die landwirtschaftliche Nahrungsproduktion davor zu schützen.

Diese Dissertation hatte das Ziel ein besseres Verständnis für den Einfluss des Klimawandels auf die Verbreitung von Schadinsekten zu erarbeiten. Für die Bearbeitung dieses Themas nutzte ich verschiedene räumliche Modellierungsansätze um damit die klimatischen Nischen von Schadinsekten und ihren Wirtspflanzen zu untersuchen. Die räumliche Darstellung dieser Nischen verschaffte neue Erkenntnisse über die potentielle Verbreitung von Schadinsekten. Das erste Kapitel untersuchte die potentielle Verschiebung der Verbreitungsgebiete von ausgewählten, als besonders gefährlich eingestuften Schadinsekten und deren bekannten Wirtspflanzen mit korrelativen Modellen. Dafür evaluierte ich die räumliche und zeitliche Dynamik von möglichen Interaktionen zwischen Schadinsekten und

ihren Wirtspflanzen mit einem Metaweb-Ansatz. Das zweite Kapitel verglich zwei komplementäre Modellierungsansätze um Unterschiede zwischen den fundamentalen und den realisierten Nischen von Schadinsekten und deren Verteilung entlang eines Temperaturgradienten zu untersuchen. Das dritte Kapitel verwendete Deep Neural Network Algorithmen um durch Insekten verursachte Schadsymptome nachzuweisen und deren Auftreten mit meteorologischen Daten zu koppeln. Dieses Kapitel brachte einen konzeptionellen Nachweis für die Verwendung von neuen Technologien hervor um das Auftreten von Schadinsekten vorauszusagen.

Diese Dissertation zeigte, dass der Klimawandel in Europa eine Veränderung der potentiellen Verbreitungsgebiete von Schadinsekten (*Kapitel 1* und *Kapitel 2*) und deren Wirtspflanzen (*Kapitel 1*) herbeiführt. *Kapitel 1* verwendete einen Datensatz von 89 Schadinsekten die als Quarantäneorganismen eingestuft sind sowie 126 Kulturpflanzen und Waldbaumarten um den hohen Druck von invasiven Schadinsekten auf den produzierenden Pflanzenbau in Südeuropa unter derzeitigen klimatischen Bedingungen aufzuzeigen. Gleichzeitig zeigte dieses Kapitel, dass die Landwirtschaft im Norden Europas von den verbesserten klimatischen Bedingungen für Kulturpflanzen profitieren könnte. In diesen Regionen werden jedoch die Erträge vermehrt durch Schadinsekten gefährdet, da dort das sich verändernde Klima das Überleben neuer Schadinsekten ermöglicht. Das zweite Kapitel verglich physiologische und korrelative Artenverbreitungsmodelle, welche trotz konzeptionellen Unterschieden gut übereinstimmten und daher für zusätzliche Robustheit der Schlussfolgerungen sorgten. Mit beiden Modellierungsansätzen konnte ich einen Temperaturgrenzwert bestimmen, welcher einen plötzlich rasch ansteigenden Zuwachs der Anzahl Schadinsekten mit geeigneten klimatischen Bedingungen begrenzt. Zusammen lieferten die Resultate von *Kapitel 1* und *Kapitel 2* starke Argumente, dass neue invasive Schadinsekten in der näheren Zukunft in Europa auftreten werden. Dadurch wird die Dringlichkeit für die Entwicklung von neuen Pflanzenschutzmassnahmen unterstrichen, um besser mit zukünftigen Invasionen umgehen zu können. Das dritte Kapitel zeigte, dass Big Data und Deep Learning zusammen neue Lösungen für die Prognose von Schadinsekten hervorbringen können. Als Beispiel zeigte ich, wie innovative Technologien für die Voraussage des Auftretens von Schadinsekten genutzt werden können und somit neue Möglichkeiten für einen nachhaltigeren Pflanzenschutz entstehen.

Zusammengefasst, tragen die drei Kapitel zu einem besseren Verständnis zum Einfluss des Klimawandels auf die potentielle Verbreitung von Schadinsekten und deren Wirtspflanzen bei. Diese Dissertation kombiniert umfassende Datensätze für Schadinsekten, Kulturpflanzen und Waldbaumarten um Regionen mit erhöhtem Schädlingsdruck zu identifizieren und präsentiert einen neuen Ansatz für die Schädlingsprognose. Die drei Kapitel liefern eine wissenschaftliche Grundlage für die Verbesserung des Pflanzenschutzes und insbesondere der Regulierung von Schadinsekten.

GENERAL INTRODUCTION

Evolution of food production

Agriculture has been central to the development of humankind, providing people with food and fibre since the dawns of civilisation (Federico, 2008). Since the 1960s, crop production drastically increased, supporting an acceleration of human population growth (Khush, 2001). This rapid development after the green revolution owes to advances in biotechnology and the development of more productive crop varieties (Pingali, 2012, Navarro, 2006; Evenson & Gollin, 2003). With advancing globalisation, large-scale mechanisation and motorisation helped to further intensify agricultural production (Knudsen et al., 2006). The expansion of arable land and irrigated surface, as well as the development and application of chemical fertilizers and pesticides to counteract against pests and pathogens, promoted further intensification of agriculture (Knudsen et al., 2006; Carvalho, 2006; Carvalho, 2017; Popp, Petõ and Nagy, 2013). However, the intensification of cropping systems fostered environmental challenges concerning land-use change, disruption of the global nitrogen cycle and pesticide use (Knudsen et al., 2006; Pimentel & Pimentel, 1990).

Covering the growing demand for food production in the near future without jeopardizing the environment requires reduced pesticide use. Chemical pesticides have been centre to the agricultural intensification in the last decades and allowed crop production to increase to the current levels (Oerke, 2006). However, excessive use of chemical pesticides has detrimental consequences on the environment and biodiversity, as well as for human health (Geiger et al., 2010; Tegtmeier & Duffy, 2004) and entails additional costs such as negative effects on non-target species (Lamichhane et al. 2015), the occurrence of pesticide resistance (Georghiou & Mellon, 1983; Carvalho, 2006) and the erosion of biodiversity (Hooper et al. 2005). To mitigate these consequences, progress towards more sustainable and less intense production is crucial (Horrigan, Lawrence & Walker, 2002). At the same time, challenges concerning global food security are pressing, since about 14% percent of the world's population still suffers from hunger and the demand for food production is expected to increase by up to 70% (FAO, 2009), while human population is predicted to reach 9 billion in 2050 (Godfray et al., 2010). To tackle these challenges and to feed the world's population without unnecessarily harming the environment, closing the current yield gap and more efficient food production must be attained (Godfray et al., 2010). Besides a systematic shift towards plant-based diets (Shepon et al. 2018), decreasing food and water waste as well as using nutrients and land more efficiently (West et al. 2014), an additional major challenge is cutting yield losses owed to pests and pathogens (Chakraborty and Newton, 2011; Riegler, 2018).

The concept of sustainable intensification has emerged to address the dual challenge of increasing food demand and sustainable production. The concept of sustainable intensification includes processes that aim at increasing productivity of cropping systems while simultaneously decreasing environmental impacts, for example by lowering pesticide inputs (Tilman et al., 2011; Garnett et al., 2013; Godfray & Garnett, 2014; Pretty and Bharucha, 2014). Novel technologies relying on modern information technology may support the goals of sustainable intensification (Tilman et al., 2011). Additionally, social trends have emerged to counteract against the excessive pesticide use and to support sustainable and local food production, aiming at reducing environmental impacts associated to agricultural production and downstream processing and marketing (Lamichhane et al., 2016; Feldmann & Hamm, 2015). Particularly, in western countries, consumer awareness for food production is growing and social trends are helping to tackle current challenges of food production (Falguera, Aliguer & Falguera, 2012). However, sustainable food systems will be increasingly challenged by climate change (Smith & Gregory, 2013) and local food production may fail to meet demand in regions where climate becomes unsuitable for crop production (Herrero & Thornton, 2013). While there is a growing demand for sustainable agriculture by decreasing pesticide use and preserving the environment, current challenges in agriculture will be amplified and new challenges will arise under climate change, threatening crop production directly and indirectly.

Food production under climate change

Human-induced climate change is strongly affecting agriculture (Lobell, Schlenker & Costa-Roberts, 2011; Bindi & Olesen, 2011) and challenging global food production and food security on various levels (Rosenzweig & Parry, 1994; Wheeler & Von Braun, 2013; Nelson et al., 2009; Parry et al., 2004). Cropping systems are expected to undergo worldwide changes, including shifts in spatial distribution due to changing patterns in temperature and precipitation (Walther et al., 2002; Lindner et al., 2010). On a global level, abiotic factors have negative impacts on crop production under climate change, but show regionally differing signals (Nelson et al., 2009; Bindi & Olesen, 2011). In temperate regions, agriculture might benefit from increased CO_2 levels and prolonged growth periods (Maracchi, Sirotenko & Bindi, 2005;

Tubiello, Soussana & Howden, 2007), leading to an increase in crop diversity, which will in turn support the resilience of cropping systems (Lin, 2011). Meanwhile, increasing frequency of droughts and other extreme weather events will threaten crop production in many regions across the globe (Rosenzweig & Parry, 1994; Wheeler & Von Braun, 2013). For example, Mediterranean regions are predicted to suffer from increasing heat and drought stress (Olesen et al., 2011) while tropical regions are at high risk due to a combination of factors, including competition for land and water, soil degradation and changes in temperature and precipitation patterns and variability (Brown & Funk, 2008; Challinor & Wheeler, 2008; Challinor et al., 2014). In fact, regions where the people are already vulnerable to hunger are expected to face drastic impacts of climate change on food production (Rosenzweig & Parry, 1994; Wheeler & Von Braun, 2013). Besides these abiotic impacts, biotic factors in form of insect pests and pathogens are threatening the agricultural sector under climate change (Deutsch et al., 2018; Battisti & Larsson, 2015; Gregory et al., 2009). With abiotic components of climate change, negative future impacts from insect pests and pathogens will likely intensify existing challenges and raise new problems for food production globally.

Insect pests under climate change

Pests and pathogens cause enormous pre- and post-harvest yield losses, which can each sum up to 10-16% of total annual crop production (Oerke, 2006; Bebber, Ramotowksi & Gurr, 2014; Bradshaw et al., 2016). In particular, the negative effects from insect pests are expected to worsen under climate change, inflicting even greater yield losses and costs associated to plant protection (Deutsch et al., 2018; Riegler, 2018). Insects are ectotherm organisms with biological rates that are highly sensitive to temperature, making them particularly susceptible to climate change (Paaijmans et al., 2013). Major problematic effects of climate change on pest species include increased metabolism, faster population growth, higher voltinism (i.e. more generations per year), and the extension of their distribution range (Porter, Parry and Carter, 1991; Bale et al., 2002; Deutsch et al., 2018). Warmer temperatures increase the performance of insects up to a species-specific thermal maximum (Deutsch et al., 2008). In tropical regions, crossing of this threshold may lead to a decrease in insect activity as species are presently close to their thermal optimum and would eventually exceed it with further warming (Deutsch et al., 2008). Meanwhile, in temperate regions insect populations are expected to benefit from climate warming, as species approach their optimal thermal conditions (Deutsch et al., 2008; Frazier, Huey & Berrigan, 2006). Additionally, survival increases in milder winters, allowing a faster population growth in the following spring (Das, Singh and Vennila, 2011). Further, faster development rates under higher temperatures and prolonged growth periods enable the development of more generations per year (Porter, Parry and Carter, 1991; Altermatt, 2010; Forrest, 2016). Together, higher metabolism and coherent increase in food consumption of individuals, combined with faster population growth will lead to greater crop yield losses (Deutsch et al., 2018). At the same time, raising pest pressure from the shift in species distributions and the spread of invasive pest species is expected (Bebber et al., 2013; Paini et al., 2016).

The warming climate supports the spread of pest species to new regions (Porter, Parry and Carter, 1991), as species track their climatic niche by moving towards newly available climates in higher latitudes and altitudes (Parmesan & Yohe, 2003; Chen et al., 2011). Particularly in higher latitude regions, minimum temperatures are expected to increase more than average temperatures (IPCC, 2007), enlarging and shifting the area with suitable conditions of many species towards higher latitudes (Bebber et al., 2013; Yan et al., 2017), because minimum temperature is the limiting factor for insect distribution in many regions (Hill, 1987; Jarošík et al., 2015). Recent examples for range expansion of pests linked to climate change have been attributed to enhanced winter survival (e.g. *Thaumetopoea pitycampa* in Europe; Battisti et al., 2005). While on regional scales, neo-native species (i.e. range expanding without human involvement; Essl et al., 2019) are expected to increasingly affect agricultural production in the near future, on a global scale, human-induced introductions bear even higher risks of invasions (Jeschke & Strayer, 2005; Wallingford et al., 2020).

Invasive species put additional pest pressure on agriculture under climate change (Pimentel et al., 2000; Ziska et al., 2011; Paini et al., 2016). The term invasive describes non-native species that have successfully overcome the four main stages of the invasion process: transport, introduction, establishment and spread (Blackburn et al., 2011). The main drivers of successful pest invasions are propagule pressure (i.e. the number of dispersing individuals: Lockwood et al., 2005), climatic suitability (Walther et al., 2009) and host availability (Niemelä & Matteson, 1996). Propagule pressure is closely linked to international trade and travel (Hulme, 2009; Roques, 2010; Bacon et al., 2012, Liebhold et al., 2006), promoting transport and introduction of pest species to new areas. Meanwhile, climate change plays an important role in lifting abiotic barriers for establishment and spread (Walther et al., 2009; Hulme, 2009; Levine & D'Antonio, 2003). Regions that were previously unsuitable are becoming more suitable with climate change, supporting establishment and spread of non-native species after the introduction to a new region (Robinet & Roques, 2010; Walther et al., 2009; Roques, 2010). For example, *Drosophila suzukii*, a polyphagous fruit pest native to Southeast Asia, was introduced to southern France and rapidly spread across Europe (Cini et al., 2014). Moreover, climate change favours establishment and spread, as ecosystems become more vulnerable to invasions due to increased disturbance, for instance through extreme weather events, creating empty niche space (Walther et al. 2009). The number of invasive insect species has increased in the recent past (Roques et al., 2009), but the species pool for potential invasive insects seems far from being saturated (Seebens et al. 2017). With higher activity and spread of insect pests, increasing need for plant protection measures in cropping systems is inevitable (Delcour, Spanoghe & Uyttendaele, 2015). In addition, contemporary measures to prevent pest species from invading new regions, including capacities for border surveillance and border control are insufficient (Poland & Rassati 2019; Cook et al., 2011; Bacon et al. 2012), because resources for plant protection are lacking (Flood, 2010). Therefore, collecting information on potential spread of insect pests is necessary and spatial modelling helps to gain knowledge on the current and future climatic suitability of these species.

Spatial modelling of insect pests

Information on the potential distribution of pest species and anticipation of new invasive species support proactive development of strategies for pest management. To investigate the distribution of pest species, two main types of modelling approaches have been applied: *inductive* and *deductive* models (Venette et al., 2010; Tonnang et al., 2017; Hill & Thomson, 2015). On the one hand, inductive modelling approaches, applied in correlative models couple the geographical distribution records of a species with environmental conditions in these locations (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith and Leathwick, 2009). These, often termed species distribution models (SDMs), are powerful tools to model the realized niche of species (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005), and have been widely used to investigate the potential distribution of invasive species (Thuiller et al., 2005; Elith and Leathwick, 2009; Jiménez-Valverde et al., 2011; Barbet-Massin et al., 2018). By projecting the modelled realized niche spatially, regions that share the environmental conditions preferred by a species are identified, informing on the potential distribution of the species under current and future climate conditions (Thuiller et al., 2005). On the other hand, deductive modelling approaches are implemented by physiological models (or process-based models), relying on physiological thresholds to identify the fundamental climate niche of a species (Venette et al., 2010; Kearney & Porter, 2004; Kearney & Porter, 2009). Thresholds marking the thermal tolerance of a species are often used for phenological models (e.g. Schaub et al., 2017), but can also be linked to spatial climate data to identify areas where a species encounters conditions within its thermal tolerance (Kearney & Porter, 2004; Kearney & Porter, 2009). Further, inductive and deductive approaches can be combined, such as in the CLIMEX model (Sutherst & Maywald, 1985; Sutherst et al. 2003), providing another approach for species distribution modelling that has been widely used to investigate potential pest distributions (Tonnang et al., 2017). The type of approach used to model a species' distribution depends of the data availability (Hill & Thomson, 2015) and both, inductive and deductive modelling approaches have been successfully applied to map areas at risk and to anticipate future invasions of insect pest species (e.g. Biber-Freudenberger et al., 2016; Fand et al., 2014).

Pest risk analyses are assessments conducted to inform decision makers on the likelihood that a pest species will enter, establish, spread and cause economic damage in a certain region, supporting the selection of risk-mitigation measures and management strategies (Venette et al., 2010; Robinet et al., 2012). Information on potential pest distributions is critical for developing such pest risk analyses (Venette et al., 2010; Eyre et al., 2012), and spatial models are applied for pest risk mapping to inform on the climatic suitability of pests in the region of interest (Eyre et al., 2012). As climate change is expected to increase the invasion success of pest species, investigating common patterns of climate suitability of invasive species, informing on spatial and temporal trends of potential invasion risk becomes increasingly important (Bebber, Gurr & Holmes, 2014). Previous studies used species distribution models to show that pest species will generally move towards higher latitudes and that an increasing number of pest species will encounter suitable conditions in temperate regions (Yan et al., 2017).

Patterns of changes in distribution of insect pest species have rarely been the centre of attention in species distribution modelling studies (but for Yan et al., 2017), and this study did not restrict pest distribution with biotic interactions in any form. In particular, the potential distribution of known host plants, reflecting host availability for pests, has never been included for future distribution modelling of insect pests. Host availability is a crucial determinant of invasion risk, and neglecting host availability will increase uncertainty of invasion risk predictions based on climatic factors alone (Niemelä & Matteson, 1996; Bacon et al., 2014).

Plant distribution will undergo changes in the future (Walther et al., 2002; Tubiello, Soussana & Howden, 2007) as crops are also limited by climatic factors (Connor, Loomis & Cassmann, 2011). Therefore, investigating the overlap between future distribution of pests and their host plants provides valuable insights and more accurate predictions of areas experiencing pest pressure in the future. Finally, climate change has shown to stimulate non-linear reactions in ecological systems (Lenton et al., 2011), resulting in abrupt shifts to potentially irreversible ecosystem states (Dakos et al., 2019), for instance the sudden collapse of pollinator populations (Lever et al. 2014). However, little is known about the temporal dynamics of the shifting patterns of pest distribution. Previous studies focused on projections to one or two future scenarios (e.g. Yan et al., 2017). With higher temporal resolution, more information can be obtained on potential linearity or non-linearity of changes. Investigating climatic niches of insect pest species will contribute to a better understanding of spatial and temporal trends of potential invasion risk.

Smart farming: seasonal pest forecasting and decision support systems

The field of precision agriculture concentrates on using information technology to manage production systems in a high temporal and spatial precision (i.e. within-field precision), aiming at increasing productivity, environmental quality of cropping systems and time- and cost-efficient farm management (Pierce & Nowak, 1999; Gebbers & Adamchuk, 2010; Zhang, Wang and Wang, 2002). In the last decades, modern information technologies have reached the agricultural sector, fostering the development of new tools to overcome challenges concerning sustainable crop production (Cox, 2002). For instance, such tools rely on sensors, drones or satellites to monitor plant growth, plant nutrients and plant pest outbreaks (Klerkx, Jakku & Labarthe, 2019). Smart farming is going a step further, using data to produce real-time decisions on farm management (Sundmaeker et al., 2016). Further, big data are expected to support the development of applications that address challenges in agriculture, including the efficiency of the full supply chain (Wolfert et al., 2017). The development of novel applications based on information technology particularly brings new opportunities for sustainable intensification (Lindblom et al., 2017; El Bilali & Allahyari, 2018). For instance, unmanned aerial vehicles with autonomous flight control (i.e. drones; Floreano & Wood, 2015) can be used to detect dry sections in a field using hyperspectral cameras, allowing efficient use of water resources (Bacco et al., 2018). Additionally, smart farming may make agriculture economically more profitable for farmers, as input resources drop and farm management becomes more time- and cost-efficient (Walter et al., 2017). Plant protection may also benefit from new technologies in the near future. With continuous implementation of drones and hyperspectral cameras, valuable information on the condition of crops is collected (Walter et al., 2017) and deep learning applications have great potential to analyse the resulting data, for instance for plant protection purposes (Zhu et al., 2018). Big data analyses have a yet unexploited potential to overcome current limitations in pest forecasting (Orlandini et al., 2020).

Developing improved decision support systems becomes more important as the demand for sustainable crop production will grow and pest pressure increases under climate change. Numerous models have been developed in the last decades to describe the occurrence and the seasonal dynamics of pest populations (e.g. Welch et al., 1978, Prues, 1983, Schaub et al., 2005; Samietz et al., 2007). Generally, such phenological models are based on thermal requirements (e.g. degree-days) and species-specific development thresholds (Damos and Savopoulou-Soultani, 2010) to describe non-linear relationships between temperature and insect development rates obtained from controlled experiments (Kemp, 2019). Although phenological models are often not designed for growers, consultants or extension services, some have been developed for pest management purposes and implemented in decision support systems (Samietz et al., 2007). These decision support systems often rely on phenological models and meteorological data to forecast insect population development under given weather conditions and aim to optimize the timing of management interventions (Strand, 2000; Olatinwo & Hoogenboom, 2014). The implementation of decision support systems has strongly benefited from improvement of computer technology, accessibility to meteorological data, and dissemination through media (e.g. internet) (Olatinwo & Hoogenboom, 2014). For example, SOPRA (www.sopra.admin.ch) is a decision support system for ten common pests of pome and stone fruits in Switzerland, relying on phenological data obtained from climate chamber experiments to simulate initial emergence and development of the relevant life stages over time, depending on input weather data (Samietz et al., 2007). While such models are extremely helpful to optimize timing, management and control measures (Samietz et al., 2007), some limitations have been reported. First, phenological data on pest species are rare and often only available for species that have been subject to research for a while (Hill & Thomson, 2015). To collect new data in climate chamber experiments is labour- and time-intensive and therefore, once established, phenological models are rarely updated. Other models are based on adult trapping and temperature measurements in the field, resulting in even greater workloads (up to four years for one species; Damos & Savopoulou-Soultani, 2010). However, climate change is affecting the phenology of insects and the synchrony of pest-host interactions (Kingsolver et al., 2011). Hence, measured relationships between temperature and development, on which phenological models rely, may be offset or outdated under climate change, resulting in unreliable predictions. Second, forecasting models often target specific pest-crop systems and are location-dependent (Donatelli et al., 2017). Current limitations lead to underuse of decision support systems by growers and other stakeholders (Mir & Quadri, 2009) and underline demand for new approaches. Compared to other branches, pest modelling seems to be lagging behind in the implementation of state-of-the-art artificial intelligence applications but is expected to bring new opportunities to pest forecasting together with big data (Orlandini et al., 2020). While deep neural networks have been applied to different issues in agriculture (Kamilaris & Prenafeta-Boldú, 2018), studies on the implementation to pest forecasting are lacking. Modern digital technologies can generate enormous quantities of data by continuous monitoring of a system (Kamilaris et al., 2017). Drones can generate large datasets (Floreano & Wood, 2015) and machine learning, particularly deep learning algorithms, are powerful tools to analyse such big data and extract valuable information from them (LeCun et al., 2015), for example to identify plant pathogens (Mohanty et al., 2016). Applying new technologies based on machine learning for pest forecasting may enhance the robustness of decision support systems and the implementation of models for new species.

Thesis outline

This thesis aims to provide a better understanding of the impact of climate change on insect pest distribution, and provides a proof of concept for the development of a new smart farming tool to better anticipate pest and pathogen damages in agricultural systems. This thesis is structured as follows:

Chapter 1 investigates how climate change affects the spatial dynamics of potential interactions between managed plants and black-listed insect pests under present and future climate conditions. In particular, I examine the potential interactions between black-listed insect pests and their host plants using a metaweb approach to ask how the linkage and exposure of crops and forest trees to insect pests may change with climate warming. I hypothesize that increasing climatic suitability for both, insect pests and their host plants across Europe will lead to larger areas of potential interaction and hence higher pest pressure posed by potentially invasive pest species. This chapter highlights a simultaneous increase of crop suitability and pest pressure across Europe, indicating that novel pest invasions may hamper the arising opportunities for crop cultivation under climate change. To attain more detailed insights on the temporal dynamics of increasing pest pressure, detailed evaluation of climatic niches of pest species is needed.

Chapter 2 explores potential pest accumulation in Europe under climate change, by comparing the expectations of an inductive and a deductive modelling approach. By investigating the potential distribution of a comprehensive set of insect pests, I explore whether model predictions of the two approaches show agreeing patterns of pest climatic suitability despite conceptual differences. Further, I investigate whether the climatic niches of these pests are gradually distributed along a temperature gradient or rather different groups can be identified. The evaluation of pest climatic niches contributed to the understanding of future pest pressure on European plant production and allowed the detection of a temperature threshold beyond which pest pressure is predicted to drastically increase. Together with *Chapter 1*, the evidence for increasing pest pressure in Europe underlines the growing demand for development of novel tools to support sustainable plant protection.

Chapter 3 presents a new framework for pest forecasting based on deep learning and big data approaches. In particular, I evaluate in a case study whether deep neural networks can be applied for pest damage recognition, and whether the occurrence of damages predicted by deep neural networks coupled with meteorological data can inform on the phenology of pest damages. This study strongly emphasizes on exploiting state-of-the-art technologies to develop new approaches for pest forecasting tools and to overcome current data scarcity of agricultural datasets.

Together, these three chapters highlight that pest pressure in Europe will increase under climate change, threatening current efforts towards sustainable intensification, and that modern technologies provide powerful tools to support the development of applications aimed at making agricultural production more sustainable.

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CHAPTER I

Crop and forest pest metawebs shift towards increased linkage and suitability overlap under climate change

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Abstract

Global changes pose both risks and opportunities to agriculture and forestry and biological forecasts can inform future management strategies. Here, we investigate potential land-use opportunities arising from climate change for these sectors in Europe, and risks associated with the introduction and establishment of novel insect pests. Adopting a metaweb approach including all interaction links between 126 crops and forest tree species and 89 black-listed insect pest species, we show that the metawebs shift toward increased numbers of links and overlap of suitable area under climate change. Decomposing the metaweb across regions shows large saturation in southern Europe, while many novel interactions are expected for northern Europe. In light of the rising consumer awareness about human health and environmental impacts of food and wood production, the challenge will be to effectively exploit new opportunities to create diverse local agriculture and forestry while controlling pest species and reducing risks from pesticide use.

Introduction

Global changes, including biological invasions and climate change, have already affected human-managed ecosystems[1] and are expected to continue to shape the productivity and diversity of agricultural and forest landscapes [2,3,4,5]. Agricultural and forest systems provide a variety of food and manufacturing resources, which are central to the functioning of societies[6,7,8]. European agriculture currently strives towards more sustainable management practices, including enhanced local food production and reduced use of pesticides[9,10]. Climate change might oppose these trends, and the design of innovative management practices will require adaptations to new environmental conditions[11]. Agriculture and forestry are particularly sensitive to abiotic changes[12]. Climate change may increase the productivity of crops and forest trees, e.g. via positive responses to higher CO_2 concentrations[13], but also increase yield losses from pests and pathogens[14,15,16]. Investigating future opportunities for crop cultivation and forest management under impending new threats from pest species is therefore crucial for addressing risks and opportunities in the agricultural and forestry sectors associated with future climate change.

At the global scale, climate change is expected to decrease crop production and hamper food security[17,18]. However, in some areas of Europe climate change may enhance productivity and provide opportunities for diversifying agriculture and forestry[19,20]. Like their natural counterparts, agricultural crop species and managed forest trees display an ecological niche of climatic preference[21], and the suitable area for growth is expected to shift with increasing temperatures[22]. Particularly in northern regions, new opportunities for intensifying agricultural and forest resource utilization are predicted for the future[12,23]. Cropping area is expected to expand towards higher latitudes, raising productivity in Northern Europe[24]. Moreover, positive *in-situ* effects, such as a prolonged growing season and increased CO_2 fertilization, could boost the productivity of agricultural systems[24] and forests alike[25,26]. For instance, the distribution range, production, quantity and quality of grapevines have been projected to benefit from climate change, thanks to higher CO_2 concentrations[27]. Overall, the beneficial effects related to climate change are expected to provide new opportunities for crop and forest tree species in some European regions, but these gains might be counteracted by greater risks from climate extreme events[26] and pest pressure[28].

Insect pests already inflict major costs to the agricultural and forestry sectors, and their impact is predicted to increase under climate change[14,15,29]. Native and recently introduced alien insect pest species cause major costs to agricultural and forest production annually[30,31]. Pre- and post-harvest yield losses can each sum up to 10–16% of total annual crop production[30]. The extra pressure from invasive pests associated with the globalization of trades is expected to increase these costs further[32]. Whereas in the past the movement of species through commercial networks and their establishment in new regions was hampered by climatic barriers[33], future climate change might lift abiotic barriers and enable the proliferation and spread of species[22]. Additionally, milder winters will enable increased survival of more insect species at higher latitudes[29,34]. Following recent warming and globalization, the number of newly established alien species, including insect pests, has been rising in Europe[35,36,37]. For instance, the polyphagous fruit pest *Drosophila suzukii* has successfully colonized Europe, and is already causing large financial losses to growers[38]. In contrast to many native pests, for which effective management practices are in place, invasive pests require the deployment of new, still largely underdeveloped control measures. Anticipating the arrival of new pest species and understanding their interactions with crops and managed forests is crucial for designing management strategies for different invasion scenarios.

Here, we adopt a metaweb approach[39,40] to study the present and future links and exposure of managed plants with their novel pests under climate change. We expect that climate change will promote: i) new opportunities for cropping and forest systems owing to an increase of areas with suitable climate for growing more diverse crops; ii) higher pest pressure caused by increasing feeding interactions from novel invasive pests on managed plants (increasing number of links), iii) greater risks caused by larger overlaps of climatically suitable areas for host plants and their pests (increasing exposure). We forecast future climatic suitability for 96 economically relevant crops and 30 forest tree species from Europe and 89 insect pest species included in lists of the European Plant Protection Organisation (EPPO). The considered pests are either recommended by experts to be regulated as quarantine species or have been recently identified as posing a risk to the EPPO region (www.eppo.int). We use species distribution modelling (SDM) and future climate scenarios in high spatial and temporal resolution to forecast climatically suitable areas for all species. We investigate the potential for plant growing under climate change within five categories ("fruit crops", "vegetable crops", "arable crops", "other crops" and "forest trees"). Coupling the metaweb with forecasted climatically suitable areas, we predict how the linkage properties between host plants and pests, and the plant species exposure are affected by climate change. We further quantify pest pressure, as the number of pests with suitable climatic habitat, for five categories of pests (“fruit pests”, “vegetable pests”, “arable crop pests”, “polyphagous pests” and “forest pests”).

Results

Changing area of suitable climate for crops and forest trees

We predict that the area of suitable climate will increase for most crops and forest tree species within Europe between 2020 and 2100. We estimate a median increase in the area with suitable climate for crops from 1,925,265 km^2 in 2020 to 2,790,484 km^2 (+47%) under the representative concentration pathway (RCP) 8.5 and 2,487,919 km^2 (+27%) under the RCP4.5 scenario in 2100. For forest tree species, the median area of suitable climate increases from 4,225,050 km^2 in 2020 to 4,366,851 km^2 (+3%) under the RCP8.5 scenario, less than forecasted under the RCP4.5 scenario (4,561,816 km^2) (+8%) until the end of the century, because of the smaller loss in southern Europe.

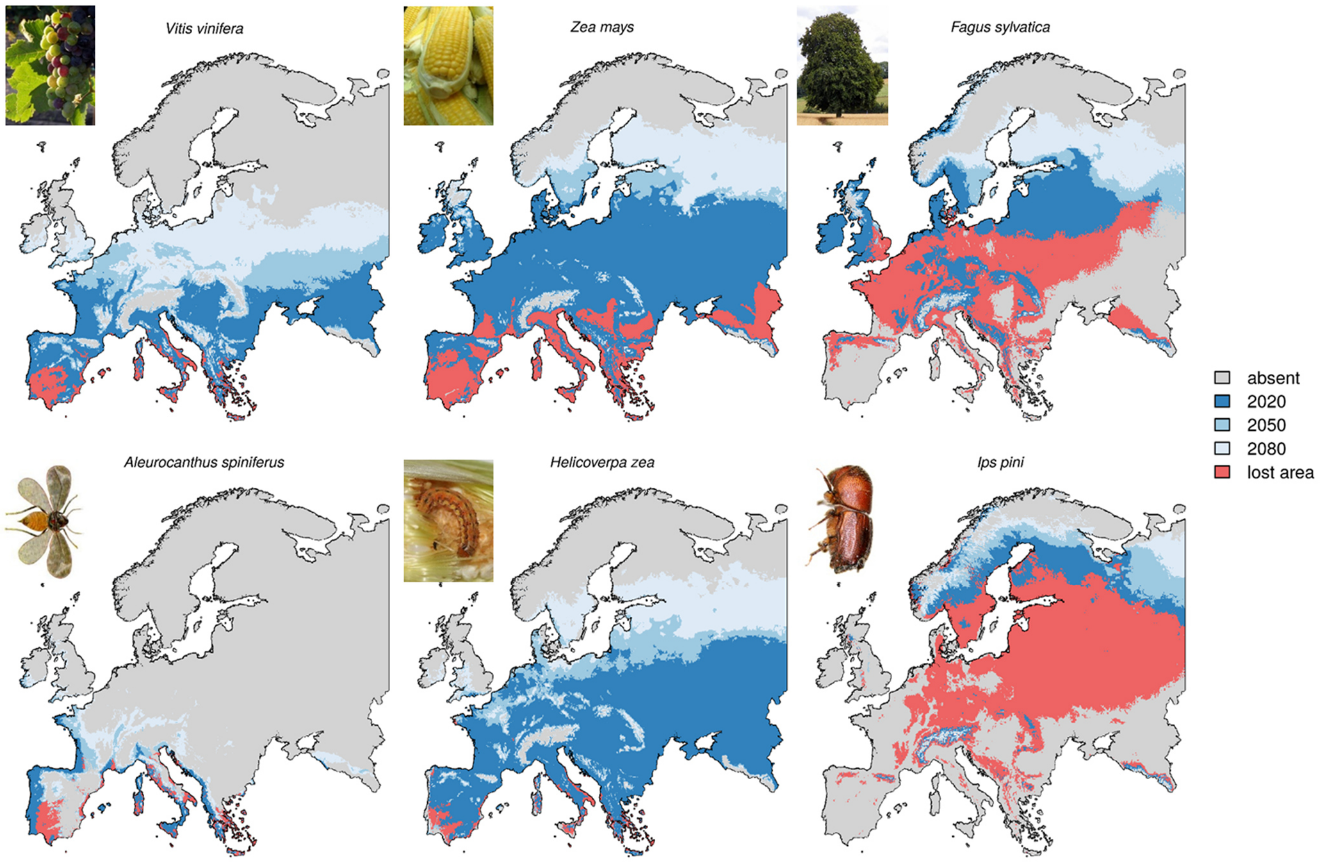

Figure 1: Predicted shifts of climatic suitability for exemplary host plant and insect pest species. Grapes (*Vitis vinifera*), maize (*Zea mays*) and European beech (*Fagus sylvatica*) show shifting climatic suitability towards higher latitudes. *Aleurocanthus spiniferus*, a fruit pest, *Helicoverpa zea*, an arable crop pest and *Ips pini*, a forest pest, also show northwards shifting climatic suitability under future climate conditions. Europe's current climate already provides suitable conditions for these pests. Red areas show climatic suitability loss from 2020 to 2100. Together the red and the dark blue area show the modelled distribution in 2020. Projections under the RCP8.5 scenario are shown here.

Images are licensed under the Creative Commons Attribution 3.0 Unported (https://creativecommons.org/licenses/by/3.0/deed.en/: Vitis vinifera: https://commons.wikimedia.org/wiki/File:Grapes_during_pigmentation.jpg; Ips pini: https://commons.wikimedia.org/wiki/File:Ips_pini.jpg), or the Creative Commons Attribution-Share Alike 2.0
Generic (https://creativecommons.org/licenses/by- sa/2.0/deed.en; Zea mays: https://commons.wikimedia.org/wiki/File:Mahane_Yehuda_Market_(9629714152).jpg; Fagus sylvatica: https://commons.wikimedia.org/wiki/File:Beech_(Fagus_sylvatica)_(19185865168).jpg; Helicoverpa zea: https://commons.wikimedia.org/wiki/File:Helicoverpa_zea_larva.jpg.) The image of *Aleurocanthus spiniferus* was offered as copyright free on http://www.ces.csiro.au/aicn/name_s/b_164.htm. All images were cropped to the fitting extent but remained otherwise unchanged.

Assuming a relationship between economic profit and climatically suitable areas, we predict increased cultivation opportunities for 82 (RCP8.5), respectively 91 (RCP4.5) out of

126 crop and forest tree species. Some of these species will have largely increased suitable climatic area and thus scope for growing economic significance. For example, in Europe soybeans currently have a gross production value of roughly 3.5 billion dollars (FAOSTAT[41]) and their suitable climate area will increase by 190% under the RCP8.5 scenario (95% RCP4.5) by the end of the century. We also predict an increase in the suitable area for many specialty crops with high market values (e.g. RCP8.5: apple +29%, grapefruit +756%, lemon lime +105%, melon +87%, tomato +42%; RCP4.5: apple +47%, grapefruit +225%, lemon lime 70%, melon +50%, tomato +23%). Meanwhile, for other economically relevant crops, the suitable climatic area within Europe is forecasted to decline substantially by 2100 under the RCP8.5 scenario (wheat -9%, maize -14% (Fig. 1), oats -44%, rye -76%, potatoes -20%), while more limited under RCP4.5 (wheat +4%, maize +7%, oats -9%, rye -28%, potatoes +1%). Forest tree species are predicted to lose suitable climatic area under steeper temperature increase (RCP8.5 *Abies alba* -73%, *Fagus sylvatica* -12% (Fig. 1), *Picea abies* -77%), but slower decline under the RCP4.5 (*Abies alba* -36%, *Fagus sylvatica* +8%, *Picea abies* -39%). We investigated the geographic differences in the change of climatically suitable areas. Our results for the five European regions highlight that new opportunities for the exploitation of crops and forest trees will open up, particularly in Northern Europe (RCP8.5: 48 species in 2020, +33 in 2100; RCP4.5: 48 +16) and the British Isles (RCP8.5: 53 +28; RCP4.5: 53 +10). In Western (RCP8.5: 85 +9; RCP4.5: 83 +9) and Eastern Europe (RCP8.5: 90 +6; RCP4.5: 90 +7), slightly more species are expected to encounter suitable climate in the future, while in Southern Europe (RCP8.5: 101 -7; RCP4.5: 100 +0) the number of species with suitable climate is predicted to decrease.

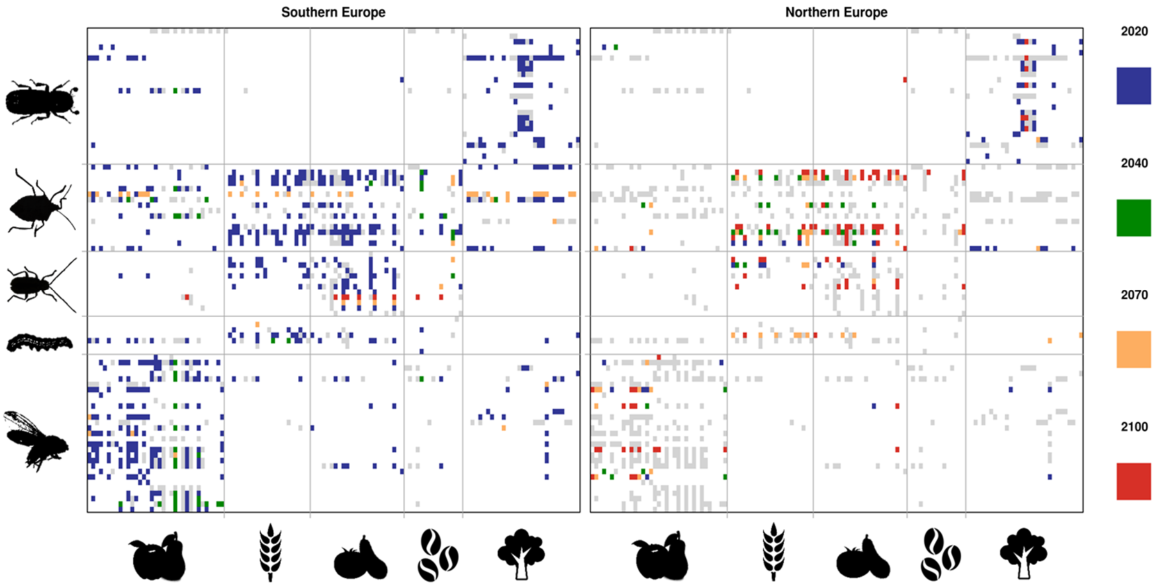

Figure 2: Predicted dynamics of realized interactions between insect pests and their host plants for Southern (left), and Northern (right) Europe under the RCP8.5 scenario. The interaction network for Southern Europe shows that most interactions are already possible under current climate conditions. Icons show different categories of pests (from bottom to top: “fruit pests”, “arable crop pests”, “vegetable pests”, “polyphagous pests” and “forest pests”) and host plants (from left to right: “fruit crops”, “arable crops”, “vegetable crops”, “other crops” and “forest trees”). “Fruit pests”, “polyphagous pests” and “forest pests” face the highest risk. Coloured points show the time step of first potential overlap between each pair of host plant and pest. In contrast, the interaction network for Northern Europe shows that many interactions become realizable only in the second half of the current century or not until 2100 (grey links). Interaction networks for other regions and RCP4.5 scenarios are shown in Supplementary Figure 1 – 5. Icons are pictures licensed under the Creative Commons CC0 1.0 Universal Public Domain Dedication https://creativecommons.org/publicdomain/zero/1.0/deed.en), the Creative Commons Attribution-Share Alike 2.0 Generic licence (https://creativecommons.org/licenses/by-sa/2.0/deed.en), Creative Commons Attribution 3.0 Unported (https://creativecommons.org/licenses/by/3.0/deed.en) or Creative Commons Attribution-Share Alike 4.0 International (https://creativecommons.org/licenses/by-sa/4.0/deed.en). Images are available at the following URLs: Forest pests: https://commons.wikimedia.org/wiki/File:Lymantor_coryli_(Perris,_1855)_Syn.- Triotemnus_coryli_(Perris,_1855)_(15286593562).png; Polyphagus pests: https://commons.wikimedia.org/wiki/File:Halyomorpha_halys_s2a.jpg; Vegetable pests: https://commons.wikimedia.org/wiki/File:CSIRO_ScienceImage_7410_A_larva_of_Helicoverpa_armigera_the_worlds_worst_insect_pest.jpg Arable crop pests: https://commons.wikimedia.org/wiki/File:Diabrotica_virgifera_LeConte,_1868.jpg; Apple: https://commons.wikimedia.org/wiki/File:Manzana.svg; Pear: https://commons.wikimedia.org/wiki/File:Pear_icon.png; Arable crop: https://commons.wikimedia.org/wiki/File:Agriculture_- The_Noun_Project.svg; Tomato : https://commons.wikimedia.org/wiki/File:Twemoji_1f345.svg; Eggplant: https://commons.wikimedia.org/wiki/File:Twemoji_1f346.svg; Coffee : https://commons.wikimedia.org/wiki/File:Coffee_beans_by_gnokii.svg; Forest trees: https://commons.wikimedia.org/wiki/File:Noun_883674_cc_Symbolon_tree_icon.svg

Increasing linkage between plants and pests

We built a metaweb recording all known interactions between host plants and insect pests for Europe. We constrained the metaweb with potential range suitability overlap in order to quantify general changes in the incidence of pests on crops, under current and future climate (Fig. 2). The measured overlap of modelled climatic suitability of host plants and pests indicates increasing number of links and exposure (as mean overlap area per link) for Europe. The metaweb filtered by suitability overlap under climate change indicates that by 2100, up to 80% (RCP4.5: 79%) of links are predicted to be possible, notwithstanding large variation among regions (i.e. Southern Europe, Western Europe, Northern Europe, Eastern Europe, British Isles; Fig. 3) and time periods (2020 – 2100). In Southern Europe, 64% (RCP4.5: 63%) of the links can already be realized under the current climate. In contrast, in Northern Europe currently only 7% (RCP4.5: 7%) of the links can currently be realized. This leaves a large potential for increase by 2100, when up to 25% (RCP4.5: 15%) of all links become possible. Most interactions in Europe affect "fruit crops" (RCP8.5: 251 +11; RCP4.5: 244 +31) and "forest trees" (RCP8.5: 176 -4; RCP4.5: 171 +8). Economically relevant crops will be affected by many more potential pest species in Northern Europe towards the end of the century (maize: +7 links under RCP8.5/ +3 links under RCP4.5; wheat +4/+3, potato +6/+3, grapevine +5/+4). We find a stronger increase in links per pest species in Northern regions. The numerous links illustrate that Southern (RCP8.5: 595; RCP4.5: 586), Western (RCP8.5: 287; RCP4.5: 297) and Eastern Europe (RCP8.5: 318; RCP4.5 297) are already potentially threatened by pest invasions under the current climate. In contrast, Northern Europe (RCP8.5: +166 links; RCP4.5: +77) and the British Isles (RCP8.5: +190; RCP4.5: +78) show a strong increase in network links under climate change, indicating that crop diversification will come at the cost of higher pest pressure. While in Southern Europe, the number of links per species decreases on average from 6.7 to 6.1, it strongly increases in Northern Europe (0.8 to 2.6) and the British Isles (1.1 to 3.2). The predicted greater occurrence of generalist pests, such as the polyphagous *Spodoptera frugiperda* and *Helicoverpa zea* contributes to the rising number of links and links per species under climate change. While in Southern Europe the links with most of their host plants are already possible under current climate, in Northern Europe, the number of links will drastically increase for both of them (*Spodoptera frugiperda*: +19 links from 2020 to 2100 under RCP8.5, +10 RCP4.5; *Helicoverpa zea*: +21 RCP8.5, +14 RCP4.5). The increase in the incidence of generalist species further causes a decrease in network specialization under climate change. Additionally, the observed modular structure is predicted to be disrupted over time, where more generalist pests will attack different categories of host plants. These trends are supported by other network metrics such as increasing partner diversity and increasing number of shared partners for host plants and pests (Supplementary Figure 6).

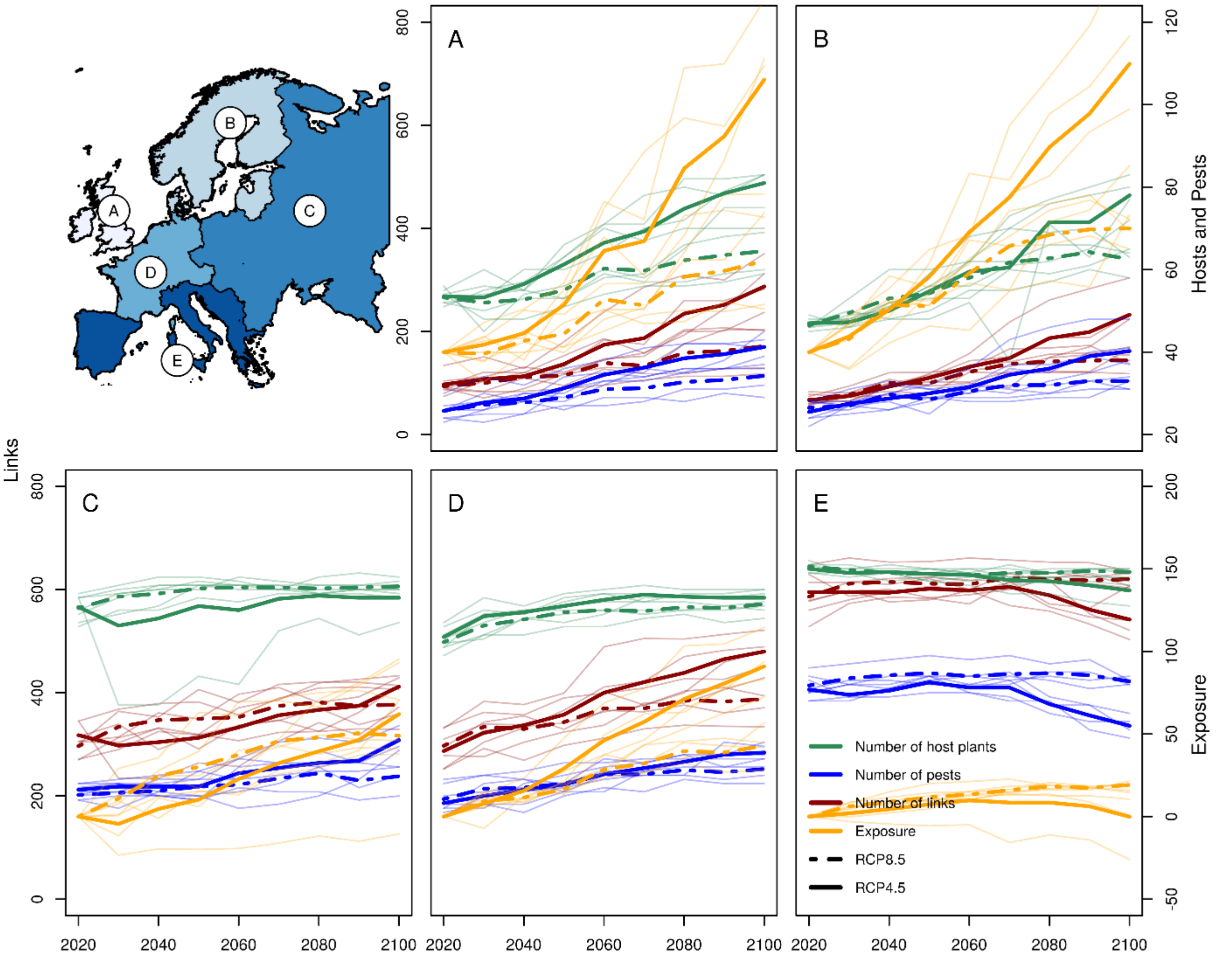

Figure 3: Network properties for European regions. European regions (A: British Isles; B: Northern Europe; C: Eastern Europe; D: Western Europe; E: Southern Europe; upper left). The graphs show properties derived from metawebs of different regions. The number of links (red), exposure, as the mean overlap area per link in percent increase (orange), host plants (green) and pests (blue) with suitable climate conditions in 5000 grid cells or more are shown per time step (2020 – 2100) for all regions (A to E). Scales for the links are shown on the left side, for host plants and pests on the right side on the upper panels, for exposure on the right side on the lower panels of the figure. Thin lines show the results of the single GCM predictions and the thick lines the medians of the 4 GCMs per scenario. Additional metrics (specialization, modularity, increasing partner diversity and increasing number of shared partners) for host plants and pests are shown in the supplementary material (Supplementary Figure 6).

Area of suitability overlap increases with climate change

Coupling the metaweb with projected climatic suitability indicates shifts in the exposure of managed plants to pests over time (Fig. 3). The mean area of overlap per link of the modelled climatic suitability of host plants and pests is predicted to increase by 51% (RCP4.5: 38%) between 2020 and 2100 in Europe. The exposure increases most in Northern Europe (RCP8.5: 173%; RCP4.5: 75%) and the British Isles (RCP8.5: 165%; RCP4.5: 57%). Also for Western (RCP8.5: 90%; RCP4.5: 43%) and Eastern Europe (RCP8.5: 60%; RCP4.5: 49%), we observe a marked increase in contrast to Southern Europe, where we predict little changes (RCP8.5: 0%; RCP4.5: is 19%). For instance, the increasing climatic suitability for some pest species promotes a marked increase of potential overlapping area with their host plants (*Spodoptera frugiperda*: +176% RCP8.5; +70% RCP4.5; *Helicoverpa zea* +88% RCP8.5; +42% RCP4.5). For different categories of host plants, we find similar patterns of slightly increasing area of overlap in all regions but Southern Europe, where we predict decreasing area of overlap for forest trees and arable crops (Supplementary Figure 7 and 8). For pest categories, we predict that forest pests will overlap less with their host plants in the future, while all other categories will have larger overlap of suitable areas towards the end of the century (Supplementary Figure 9 and 10). Although the climatic suitability drops for some crops, the area of overlap of these crops with their pests is nevertheless predicted to increase, as found for maize (RCP8.5: +110%; RCP4.5: +39%), wheat (RCP8.5: +135%; RCP4.5: +40%) and potatoes (RCP8.5: +80%; RCP4.5: +44%).

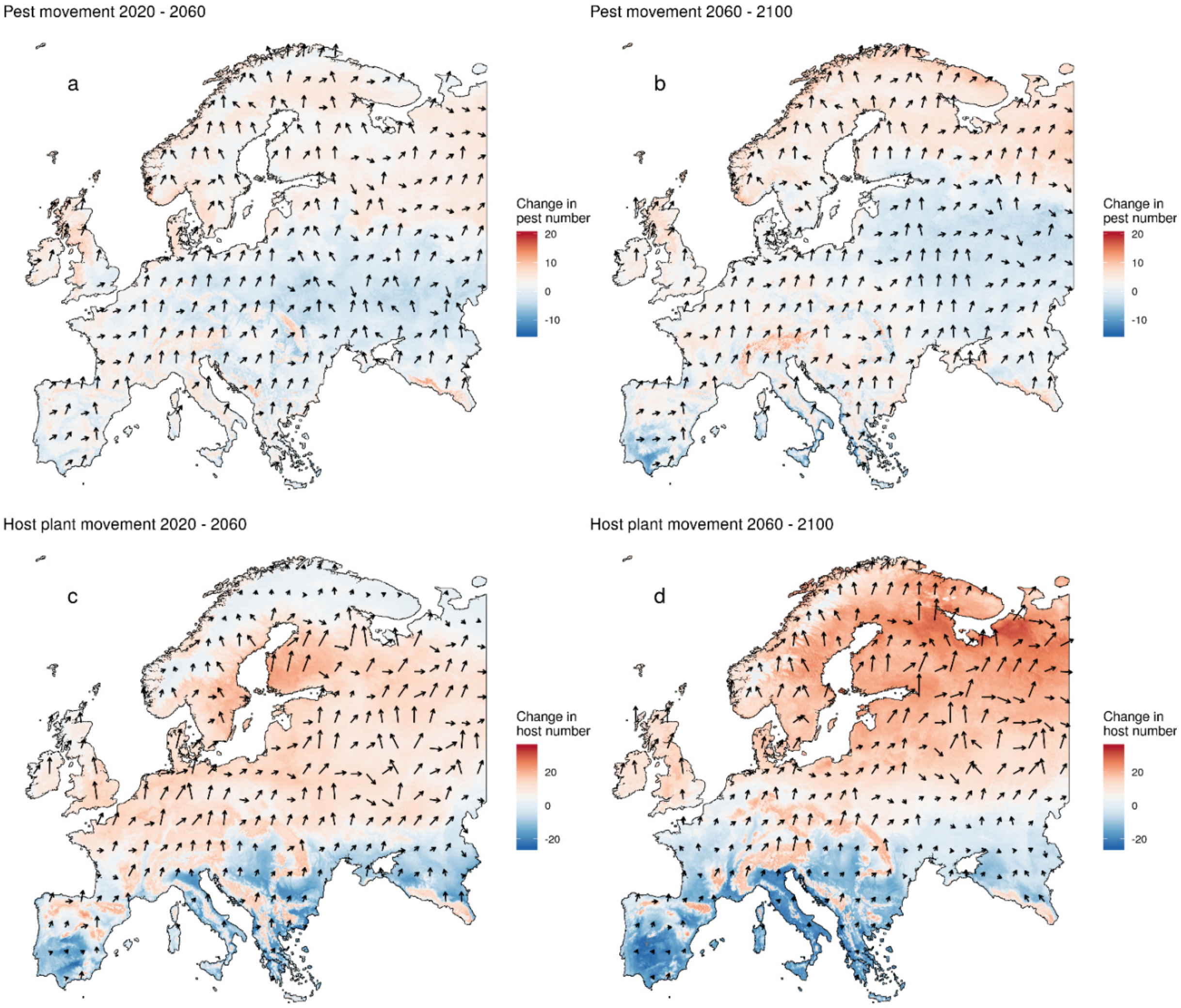

Figure 4: Climatic suitability shift for pests and host plants. Arrows show for each grid cell the average direction of climatic suitability shift over all species. For each species, we calculated the direction from where each newly suitable grid cell can be reached from its closest suitable grid cell in the previous time step. The length of the arrows is proportional to the number of new colonisations of each grid cell. The coloured maps show the change in total number of pests (top) and host plants (bottom) with suitable conditions during the time steps of 2020 – 2060 (left) and 2060 – 2100 (right). Red shadings indicate an increase of the number of species with suitable climate; blue shadings indicate decreasing numbers. Climatic suitability shift and change in number of species are shown for the RCP8.5 scenario (see Supplementary Figure 11 for RCP4.5).

Changing area of climate suitability for pests

Overall, the median area with suitable climate for insect pests (2,491,321 km^2 in 2020) will increase under climate change associated with a northward expansion of pest species. We forecast an average increase in the suitable area for pest species of 294,176 km^2 (+12%) under the RCP8.5 scenario and 229,981 km^2 (+9%) under the RCP4.5 scenario. Most of the considered pests already have suitable climatic conditions in Europe. In particular, Southern Europe (RCP8.5: 71; RCP4.5: 71) is already threatened by many of the pests on the EPPO Lists. In Northern Europe (RCP8.5: 26 +14; RCP4.5: 27 +5), Western Europe (RCP8.5: 43 +13; RCP4.5: 44 +8), Eastern Europe (RCP8.5: 47 +11; RCP4.5: 45 +6) and the British Isles (RCP8.5: 25 +17; RCP4.5: 26 +9), pest pressure will increase until 2100 (Fig. 3). Under the RCP8.5 we predict increasing suitable climate area for 60 of 89 pest species (71 under RCP4.5), and hence important potential expansions such as for the fall armyworm (*Spodoptera frugiperda)*, which will increase by 81% (3,341,038 km^2 under current conditions; 51% under RCP4.5), corresponding to additional 2,758,535 km^2 (1,676,514 km^2 under RCP4.5). We quantified the dynamic shifts of climatic suitability for host plant and pest species from and to each colonized grid cell in Europe between 2020 – 2060 and 2060 – 2100 (Fig. 4). The shift of climatic suitability for host plants shows a gradient towards higher latitudes, underlining the opportunities arising in northern regions in the second half of the century. Meanwhile, the shift of climatic suitability for insect pest shows no clear south-north gradient, possibly because of more complex and diverse climatic niche shapes of pest species. Consequently, the dynamic of the shift of insect pest species is expected to be more idiosyncratic than that of their host plants under climate change. We observe a slight decrease of the number of pest species in central and northeastern regions, caused by the gap in climatic niches between cold-adapted pests and more warm-adapted pests (Supplementary Figure 12). While cold-adapted species will move further north with increasing temperatures, warm-adapted species are lacking behind. Finally, we analysed the shift in centroid position of all modelled ranges of host plants and pest species by measuring the direction and distance of the movement between 2020 and 2100 (Supplementary Figure 13 and 14). The centroid analysis shows a median distance of 519 km, and speed of 6.5 km/year for pests under RCP8.5 (240 km; 3.0 km/year for RCP4.5), values that are consistent with published estimates of dispersal capacity[42]. The analysis indicated a median distance of 588 km for host plants, resulting in a speed of 7.3 km/year (269 km; 3.4 km/year for RCP4.5).

Discussion

The metaweb approach adopted in our study indicates a general increase in susceptibility of managed plants to pests under climate change owing to 1) an increase in the number of links between crops, forest trees and their pests, and 2) an increase in the area of climatic suitability overlap between pests and plants, which will challenge the benefit of climate change on agricultural diversification. In contrast to the increase in potential distribution for single crops (e.g. for maize[43]), here we show a general pattern of increasing climatic suitability for a wide variety of crops and forest tree species, indicating that climate change will favour diversification of European plant production across different subsectors. While in Southern Europe future climate will become increasingly unsuitable for staple crops like wheat, maize and potatoes, future suitable areas are identified in northern countries, partly offsetting the loss in the South. In northern European regions, the potential for growing more valuable crops and trees provides scope for enhanced economic profit. For example, grapes are currently harvested on 3,429,137 ha in Europe, resulting in a gross production value of roughly 30 billion dollars (FAOSTAT[41]). We forecast that the suitable climate for growing grapes will increase by 136% under the RCP8.5 (71% under RCP4.5) by 2100. If the production area increases in proportion, gross production values could increase by roughly 22 to 40 billion Euro. While the agronomic and economic implications are far more complex, we highlight a wider range of opportunities for growing crops across Europe under climate change. Since multiple crops cannot spread simultaneously into new areas, the decision of realizing new crop potential will depend on the market prices, consumer demands, regulatory frameworks and cultivation decisions at the farm level.

Increasing climatic suitability and associated positive effects for host plants might be offset by simultaneously increasing number of links between managed plants and pests at their degree of exposure. By quantifying changes in interactions between pests and their host plants under climate change within a metaweb, we demonstrated that increasing plant climatic suitability is accompanied by increasing pest pressure across Europe. Using a metaweb including 89 pests and 126 host plants allows to investigate the change in the system as a whole, including a variety of climatic niches (Supplementary Figure 12) and all European regions. We show how the web of agricultural pests and cultivated plants is forecasted to change, rather than predicting the suitable climate for single pests and crops [e.g. 43,44]. We found that polyphagous pests will most expand the interaction area with their host plants, while for forest trees exposure to pests decreases on average (Supplementary Figure 9). Generalist species affecting crops will benefit most from warmer temperatures with a larger potential distribution and increasing number of possible links. This is underlined by several metrics of the interaction network (decreasing modularity and specialisation, and increasing partner diversity and number of shared partners), showing that the average number of interactions per pest and the links of pests with other categories of hosts will increase in most regions, while specialisation will decrease. The invasion success, and thus the nature and extent of pest threats, and the damage caused depend on host availability[45,46], while larger areas of overlap between plants and pests have a larger potential for interactions and therefore larger population sizes and higher invasion risk[47]. We observe a sharp rise of exposure to pests, especially in Northern Europe and the British Isles. Although northern regions are predicted to benefit most from increasing climatic suitability for crops and forest tree species under climate change[19], they will also become more targeted by pest invasions. Global changes in climatic suitability of pest species has been shown with correlative models, indicating higher pest pressure in high latitude regions[48], and rising pest pressure has been associated with increasing metabolic rates of pests and therefore increasing crop losses in warmer climates[14]. Our metaweb approach corroborates this trend, and adds a thorough quantification of the nature of the risks in terms of link distribution and their strength. Seizing new opportunities will require weighting the benefits of new exploitation opportunities against the costs of co-occurrence of the novel crop or tree species and their associated novel pest species, whereby the latter may also collaterally affect other host plants.

The general pattern of pest range shift to higher latitudes will likely be associated with increasing yield losses and pest management costs[48]. Our approach to model the change in climatic suitability with a high temporal resolution of climate change illustrates the potential direction and speed at which species can be expected to spread. We show that under current climate conditions, most species could invade parts of Southern and Western Europe, and from there spread north-east with the changing climate. The predicted median speed of 6.5 km/year for the RCP8.5 emission scenario (RCP4.5: 3.0 km/year) is well in line with previous estimates for invasive insect species. Roques et al. (2016) estimated spreading rates of accidentally introduced species of 3.5 km/year, but results varied widely among insect orders (e.g. 7 km/year for Coleoptera)[42]. Assuming that the EPPO lists are proportionately representative for the categories of pests in the pool of pest species, we predict that most interactions will occur for pests of “fruit crops”, “vegetable crops” and “forest trees”, indicating that these are the crop, respectively tree categories most jeopardized by pest invasions. The number of interceptions at European borders between 1995 and 2004 show that Hemiptera (sub-order Sternorrhyncha), Diptera and Coleoptera are the orders intercepted most often of all insect pests[49]. In our dataset, 60 species belong to these orders and 47 of these species are either “fruit pests”, “vegetable pests” or “forest pests” (Supplementary Data 1). This indicates that our selection reliably reflects current propagule pressure and that the number of included species allows representing these different categories adequately. Further, we point out the difference in predicted pest pressure between the two RCPs. The median area of the modelled distribution of pests and the median overlapping area under the RCP4.5 scenario increase much less than under the RCP8.5 scenario (Supplementary Figure 12). Northern regions might therefore suffer from fewer pest invasions under the RCP4.5 than under the RCP8.5 scenario (e.g. Northern Europe: +14 RCP8.5, +5 RCP4.5; British Isles: +17 RCP8.5, +9 RCP4.5), thus corroborating the urgency of policies aimed at restricting CO_2 emissions in the near future.

An alarming implication of our results is that in large parts of Europe (i.e. mainly Southern and Western Europe) many of the invasive pests included in our analysis can survive under current climate conditions. In these regions, many host plants of these invasive pests can already be grown, and most network links are thus feasible, highlighting that invasion risks are an impending reality with the potential to severely disrupt the ecology and economics of managed ecosystems. This finding underscores the urgency of rapidly deploying support to phytosanitary services in Mediterranean countries. Pathways of insect pest invasions are often associated with accidental introductions by international trade, cargo movement and individual travel[35,50,51]. Once introduced and established in a new region, a pest might spread further to other regions with suitable conditions. Interception statistics from cargo control show that live plant imports bear an especially high risk of transporting insects[52]. Phytosanitary services have strict regulations for the inspection and control of live vegetal goods[45,53], which will become even stricter in the European Union under the Regulation EU 2016/2031. However, international trade and travel have reached such a large volume, that screening and inspecting all potential routes of invasions is no longer feasible[51]. Finally, we emphasize the importance of preparing for scenarios where pests overcome natural barriers by human-aided transport. As noticed before, Southern Europe is already an entry gate for many subtropical pest species such as *Aleurocanthus spiniferus* (Fig. 1).

In conclusion, we showed that the structure of the plant-pest metaweb will be altered under climate change, favouring greater diversity of managed plants and incidence of pests, especially of generalist ones. In Europe, climate change could overall have beneficial effects on the diversity of crop production. However, to exploit this potential, it is crucial to monitor and prepare for potential collateral risks of pest pressure. Pest pressure presents a severe threat to European agriculture and forestry already under the current climate and will keep rising in the future. Reaping the benefits from the newly arising opportunities while minimizing the costs associated with the risks of climate change requires strong efforts and collaborations among all stakeholders in the food and wood production chains.

Methods

Data collection

We considered all crops for which distribution ranges are available from Earthstat[54,55] (www.earthstat.org) and economically important forest tree species of Europe. We downloaded distribution ranges for crops as raster from Earthstat[54,55] and for forest trees as shapefiles from EUFORGEN (www.euforgen.org) whenever available and presence records from GBIF (www.gbif.org) for all other species. We only included crops and forest trees listed as host plants for at least one of the pest species included in the EPPO plant quarantine lists (Alert, A1, A2; www.eppo.int). Vectors of plant pathogens were not considered. Occurrence records for pests were collected from various databases and from the published literature (see complete list of host plants and pests in Supplementary Data 1 and 2). We considered only species reported as present in fewer than five European countries in order to abstract from species already established on the continent, and strengthen the focus on pests to be expected in the future. We did not consider occurrences from stepping stones such as greenhouses and other structures that provide protection from unsuitable climate and thus promote the proliferation and spread of invasive species by enabling them to bridge unsuitable conditions and build up early generations in spring (e.g. *Tuta absoluta*[56]). Coordinates of occurrence records were mapped for each individual species and checked for unreasonable records by comparing with EPPO PQR database (https://gd.eppo.int) distribution maps, which show for each country if a species is present or absent. To prevent from multiple records per cell and reduce sampling bias, we filtered the data with a minimum distance between each pair of records. With the remaining occurrence records the geographic extent of the species range is represented as reliably as possible (i.e. records in native and invasive range). To secure adequate SDM performance, we excluded species with fewer than 24 occurrence records (8 records per explanatory variable). In total, 128 host plant species and 94 insect pest species met these criteria.

Species distribution modelling

SDMs were calibrated using ensembles (unweighted average) of four widely used modelling techniques (Generalized linear models (GLM), Generalized additive models (GAM), Gradient boosting machine (GBM), RandomForest (RF)) or a subset. We used a pseudo-absence approach, which is widely recognized as a solution for overcoming the lack of species absence data[57]. For each species, we randomly sampled 5,000 pseudo-absences from biomes in which the species' occurrence records lay. We down weighted the pseudo-absences to reach a prevalence of 0.5. In a first step, we projected the models globally to check the potential distribution under current climate visually. For future projections, we projected our models only to Europe. To evaluate model performance, we used the area under the ROC-plot curve (AUC)[58,59] and true skill statistics (TSS)[60]. We used a split sample approach (70% calibration data and 30% evaluation data) with 20 repetitions. Models were considered to have a reliable performance with AUC scores > 0.7[61] and TSS values > 0.4[62]. Models with AUC < 0.7 were not included in the ensemble. Five pest species and two crop species with unsatisfying evaluation metrics were excluded from the analysis (see Supplementary Data 3 – 6 for model performances).

Using SDMs to model the climatic suitability of pests and plants is a common and widely accepted approach. However, we are well aware of shortcomings when applying SDMs to invasive species. Invasive species tend to occur in a broader climatic niche in their invasive range than in their native range, for example because of the lack of natural enemies. This may lead to an underestimation of the region of climatic suitability for pests when only the native climatic niche is modelled. To overcome this caveat, we covered the native and invasive range of pests by including distribution records from their entire known range whenever possible[63] (see Supplementary Data 7 for more detailed description). Further, we omitted biotic factors and dispersal limitations in our models. While we can assess the climatic niche of the species, in reality their distribution may be constrained by these factors. For host plants, the soil properties are also a major restricting factor. Therefore, we expect to overestimate potential distributions and the changes in the network. However, this limitation should mostly impact forest species because the movement of crops and pest species is affected by agronomic decisions, and thus only partly dependent on dispersal abilities. Finally, irrigation has a large impact on the distribution of many crop species. As precipitation patterns will differ from current conditions under climate change, water scarcity may limit crop irrigation in many parts of Europe during growth periods, restricting the distribution of crops. However, these changes are difficult to predict and beyond the scope of this study. Here, we addressed the issue by comparing models including both temperature and precipitation variables with models based on temperature alone. We found good agreement between the two approaches and hence applied SDMs based on only temperature variables to crops.

Climate data and climate change scenarios

For historical climate data, we used the CHELSA V1.2 dataset[64] (www.chelsa-climate.org) with a 2.5 arcmin (~ 5 km) resolution. For future scenarios, we used model output statistics in combination with mechanistic downscaling (the CHELSA algorithm) to calculate mean monthly maximum and minimum temperatures, as well as monthly precipitation sums at a ~ 5 km spatial resolution globally for the years 2006-2100. Projected future climate variables were taken from four global circulation models (GCMs) driven by two scenarios of representative concentration pathways (RCP4.5 and RCP8.5) in a factorial manner. The four selected models originate from the CMIP5 collection of model runs used in IPCC's 5th Assessment Report[65]. Different GCMs are, however, often based on similar code, and hence generate similar output[66,67]. We therefore chose models characterized by only a small amount of interdependence to allow for a good representation of uncertainty in climate projections. Model selection was based on model interdependence in ensembles[67]. Data were taken from the following four models: CESM1-BGC, run by the National Center for Atmospheric Research (NCAR); CMCC-CM, run by the Centro Euro-Mediterraneo per i Cambiamenti Climatici (CMCC); MIROC5, run by the University of Tokyo; and ACCESS1-3, run by the Commonwealth Scientific and Industrial Research Organization (CSIRO) and the Bureau of Meteorology (BOM), Australia.

We aggregated current climate data (1979-2020) in five-year time intervals, from which we extracted climate data for all presence and absence records of pests, considering their sampling year if available. Records older than 1979 were coupled with the first time step. Records with no sampling year were coupled with an average of the historical data. We coupled host plant records with a baseline of future climate (2006 – 2020) for each GCM and RCP. Additionally, we considered the resolution of the presence records. For low-resolution records (lower than 2.5 arc min), we extracted climate data from aggregated variable layers (5 arc min). Presence records with a precision of less than 5 arc min were excluded. For model projections, we aggregated time series of future climate (2011 – 2100) into 10-year time steps. For host plant SDMs, we used subsets of the following five explanatory variables: mean annual temperature, temperature seasonality, growing degree-days above 5°C, annual precipitation and precipitation seasonality. In parallel, we ran models for all crop species without precipitation variables. Due to crop irrigation, precipitation might be an unreliable predictor of the distribution of crop species. We tested both approaches and found very similar results. For the final analysis, we thus used models based on temperature alone. For pest SDMs, we chose the following variables: minimum temperature of the coldest month, growing degree-days above 5°C, annual precipitation and precipitation seasonality. For 15 pest species, we added temperature seasonality to the explanatory variables and used a subset of the five variables to reach better model performance. All explanatory variables were chosen based on ecological significance[68,69]. We chose the variables based on ecological importance rather than statistical information criteria[70] (see Supplementary Data 1 and 2 for the variables included for each species). Overall, we followed the recommendations to meet sufficient best practice standards of species distribution modelling[70].

For further analyses, we applied a binary classification of the climatic suitability to each model output. We used the sensitivity-specificity sum maximization approach to define the threshold that separates suitable from unsuitable climate[71] (R package *presenceAbsence* 1.1.9[72]). To apply binary classification to the ensembles, we used the average of the thresholds of all individual models included in the ensemble. Further, in all models we restricted the area of crop distribution with a cropland mask derived from Earthstat[54,55]. We analysed the number of species per grid cell within Europe by overlaying binary model outputs of all species. We measured the area of suitable climate for each species as the sum of the specific area of all cells classified as suitable. For each European region (i.e. Southern, Western, Eastern and Northern Europe and the British Isles), we calculated the number of species with suitable climate conditions in at least 5,000 grid cells (representing about 10% of the median agricultural surface of the different regions) per time step.

Metawebs

We generated a metaweb[39,40] recording all known interactions between pests and their host plants, which defines all possible network links. For each pest, we used a list of host plants given in the EPPO database on quarantine pests (http://www.eppo.int). We investigated all potential links for each time step by testing whether modelled distributions of host plants and pests overlap in at least 5,000 grid cells. We did not consider host shifts that can occur in the invaded range, climate-driven evolutionary change, or phenotypic plasticity in either host plants or pests, their interactions and their interactions with other species[73]. We measured the area of overlap in the same way as the area of suitable climate (see above). For each European region, we counted the interactions that occur in at least one grid cell. To summarize the numbers from the different GCMs we calculated the median of each metric. We calculated exposure as the mean of the overlap area of all links for each timestep. Modularity, specialization, partner diversity and number of shared partners were calculated with the R package *bipartit*e 2.13[74].

Climatic niches

Climatic niches of host plants and pests were computed based on the worldwide modelled distribution under current temperature. For each species, we isolated all grid cells predicted as suitable by our models and obtained the annual minimum temperature for these grid cells for current conditions. The range of occupied minimum temperatures was then used as the climatic niche over minimum temperature. For the borders of minimum temperature in Europe, we obtained the minimum and maximum value of the annual minimum temperature raster of Europe for 2020, 2060 and 2100 as a mean of the four GCMs.

Spatial analysis of shift in climate suitability

To calculate the direction of shifts of climatic suitability, we extracted newly suitable grid cells for each species and all 10-year time steps. For each newly colonized grid cell, we identified the closest already occupied grid cell in the previous time step and measured the direction from there to the focal cell in a 25 km resolution. We averaged the direction for each grid cell over all species and counted the number of species colonizing each grid cell. We displayed the direction in a 250 km resolution to highlight general regional patterns. Further, we averaged the direction and number of colonization of the single time steps for 2020 - 2060 and 2060 – 2100. We did not apply a crop mask to the modelled distribution of crops for this analysis because excluding grid cells led to unreliable averages during the interpolation of the direction. The analysis of the shift of climatic suitability is a qualitative representation to investigate general patterns and, therefore, small-scale inaccuracies might occur. Centroids were calculated as the latitudinal mean and the longitudinal mean (weighted with the cosine of latitude) of all occupied grid cells. All analyses were done in R version 3.5.1[75].

Statistics and Reproducibility

For producing random numbers, we applied the set.seed function of the R package base (version 3.5.1)[75] to enable reproducibility.

Data availability

Climate data is available from www.chelsa-climate.org. Crops distribution maps available from www.earthstat.org, forest distribution maps from www.euforgen.org. Pest distribution records were gathered from published literature and databases and are available from the corresponding author upon request. All source data underlying the Figures 1-4 are available in Zenodo with the identifier https://doi.org/10.5281/zenodo.3746103[76]

Code availability

The R codes for species distribution modelling, calculations of the results and analysis are available from https://doi.org/10.5281/zenodo.3746103[76].

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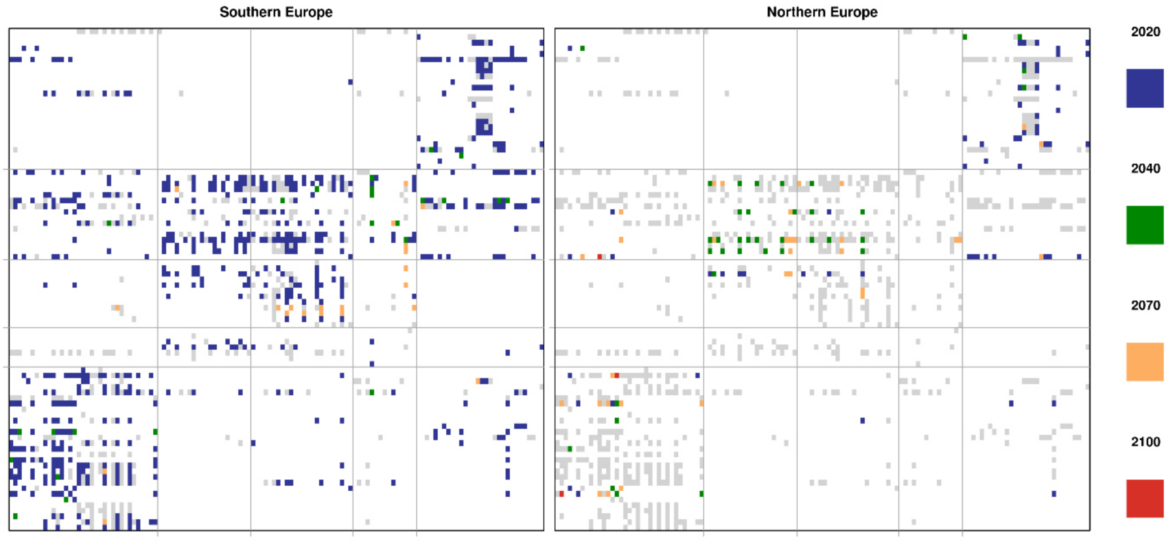
Author contributions

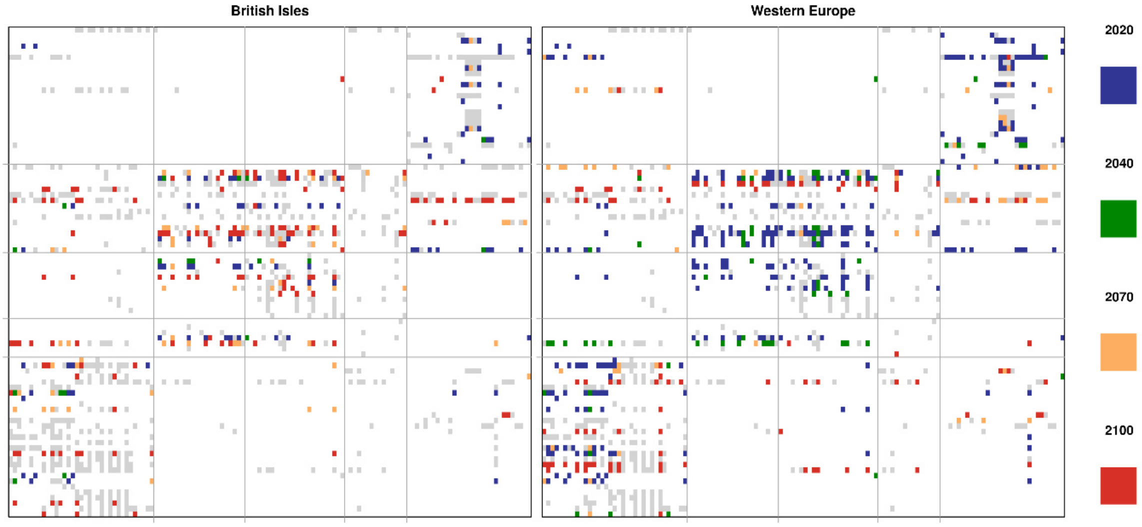
M.G. contributed to conceiving ideas, gathering distribution data, establishing and running models, performing analysis and writing the manuscript; D.M. contributed to conceiving ideas and writing; P.C contributed to conceiving ideas and writing; D.N.K. provided climate change scenario data; L.P. contributed to conceiving ideas, establishing models and writing. All authors gave final approval for publication.

Supplementary material

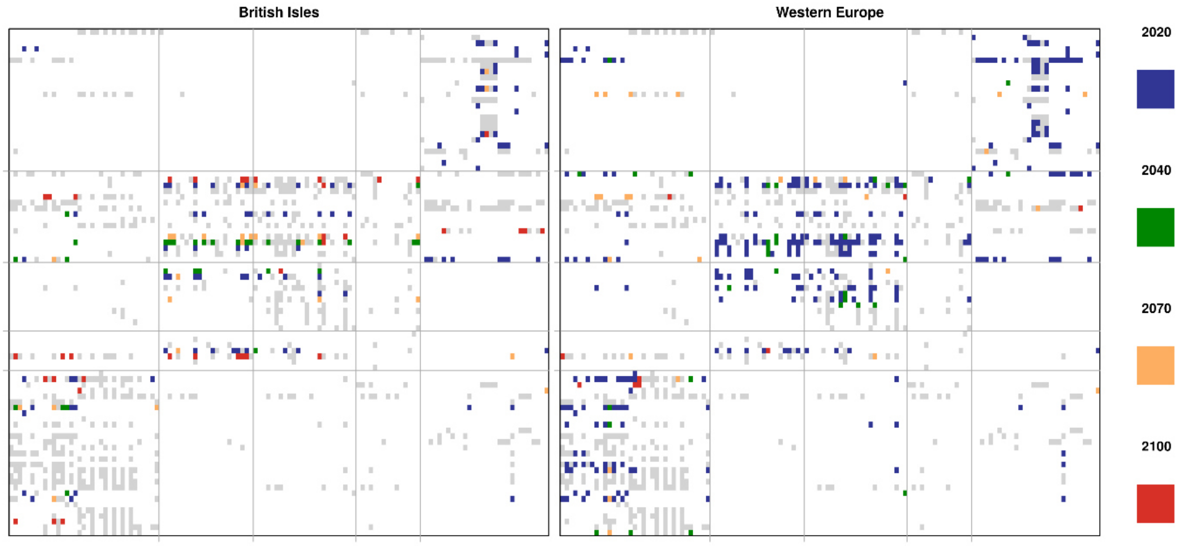
Supplementary figures



Supplementary Figure 1: Evolution 2020-2100 of the interaction network for Southern (left) and Northern Europe (right) under the RCP4.5 scenario. The geographic extent of the regions is defined in Fig. 3.



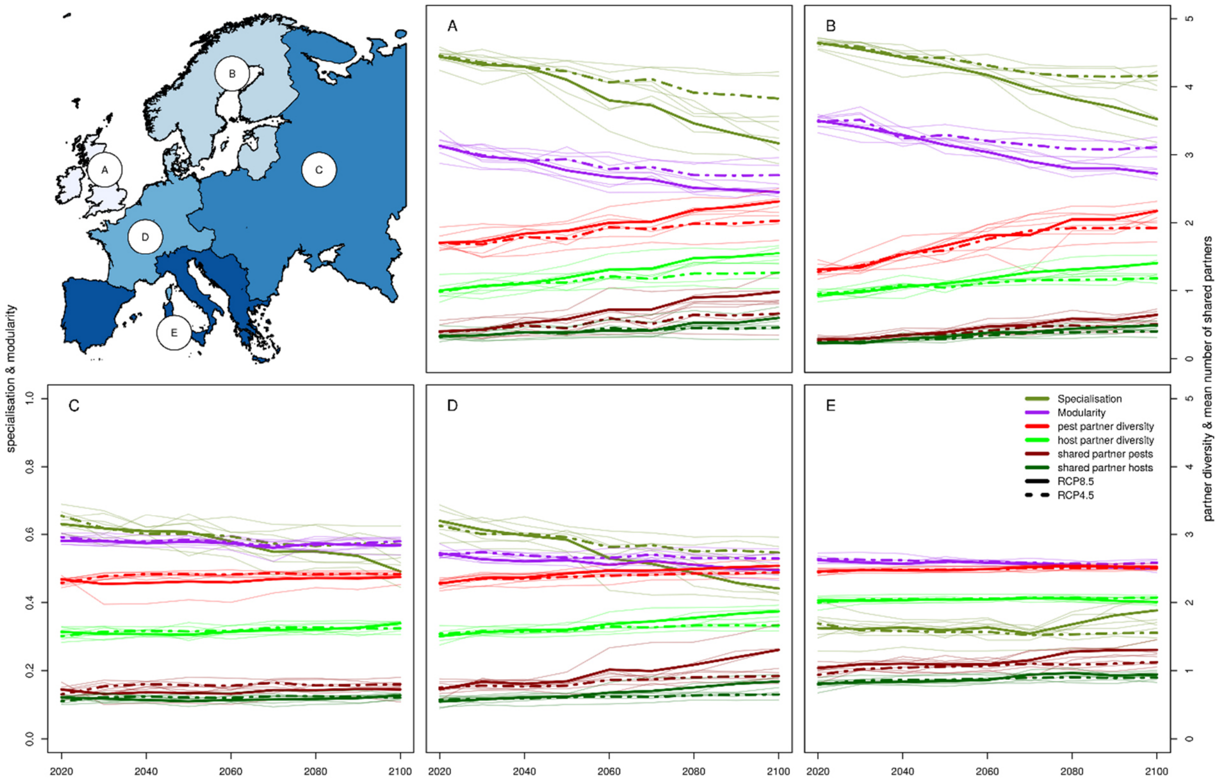
Supplementary Figure 2: Evolution 2020-2100 of the interaction network for the UK (left) and Western Europe (right) under the RCP8.5 scenario.



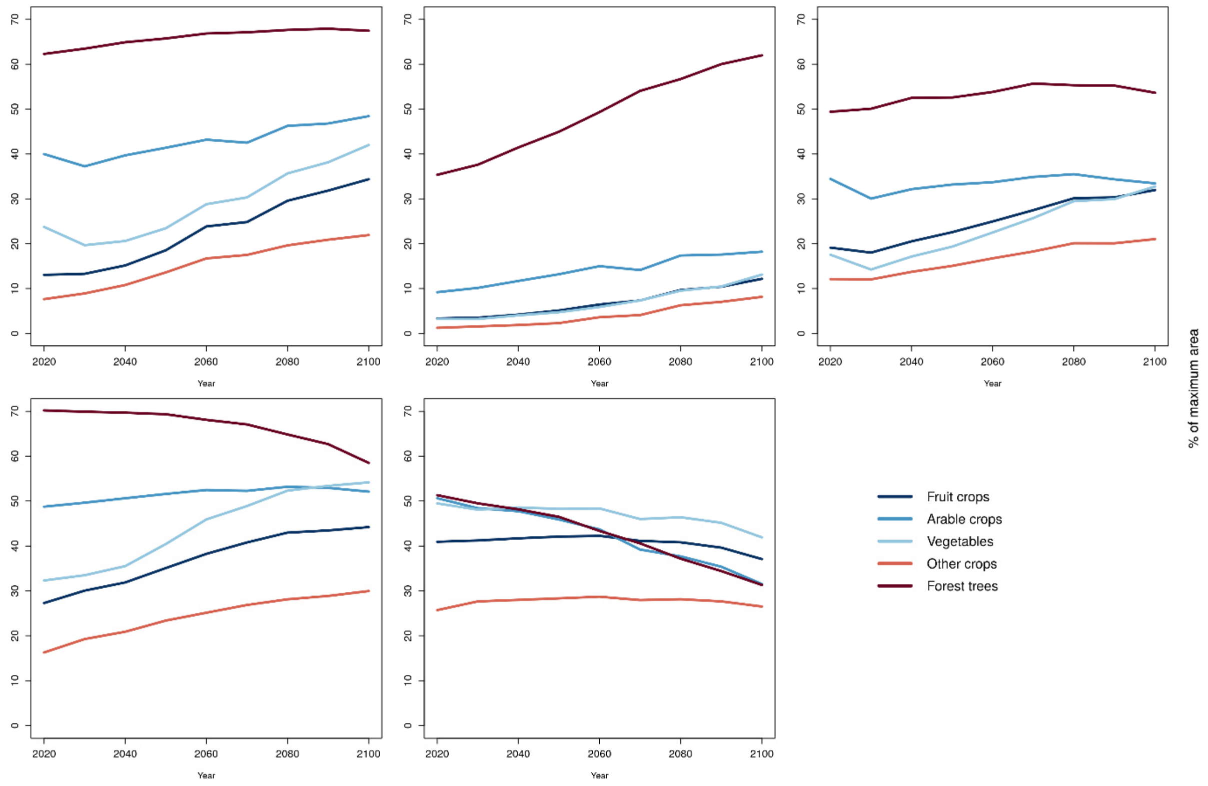
Supplementary Figure 3: Same as supplementary Fig. 2 but for the RCP4.5 scenario.

Supplementary Figure 4: Evolution 2020-2100 of the interaction network for Eastern Europe (left) and total Europe (right) under the RCP8.5 scenario.

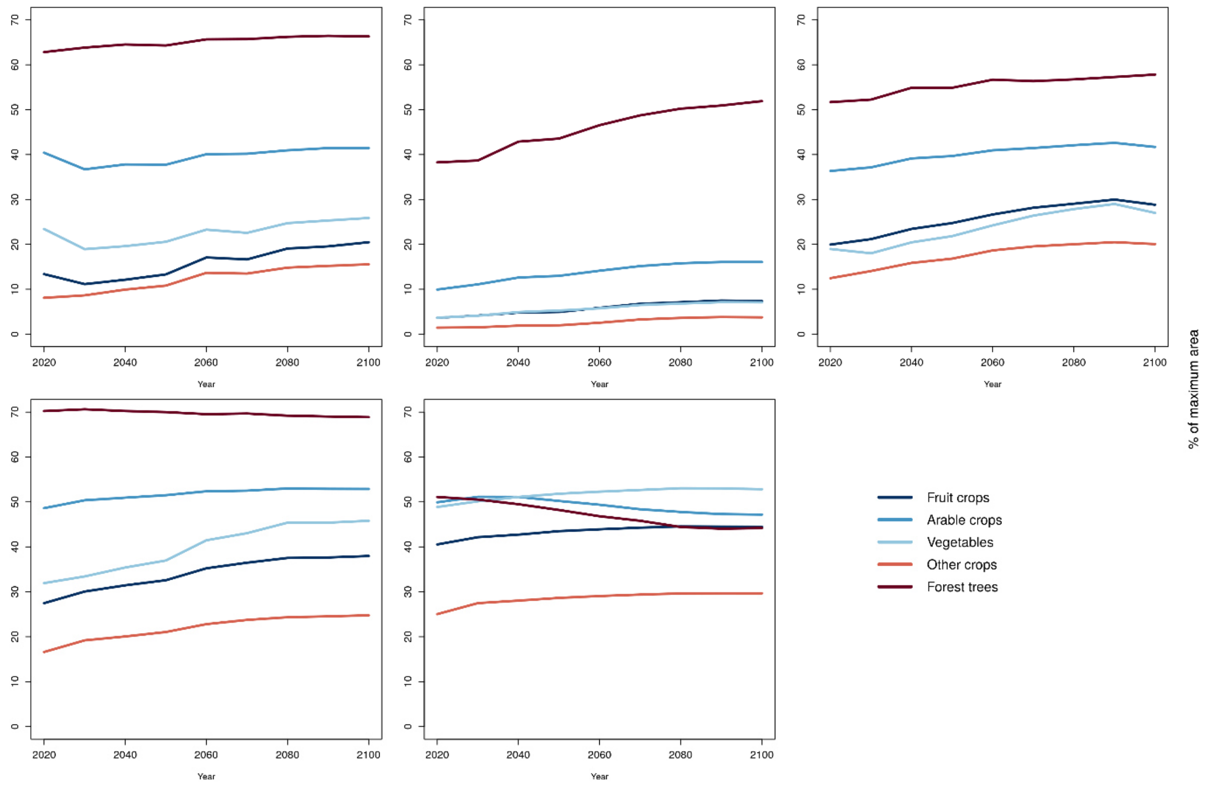
Supplementary Figure 5: Same as Fig. S4 but for the RCP4.5 scenario



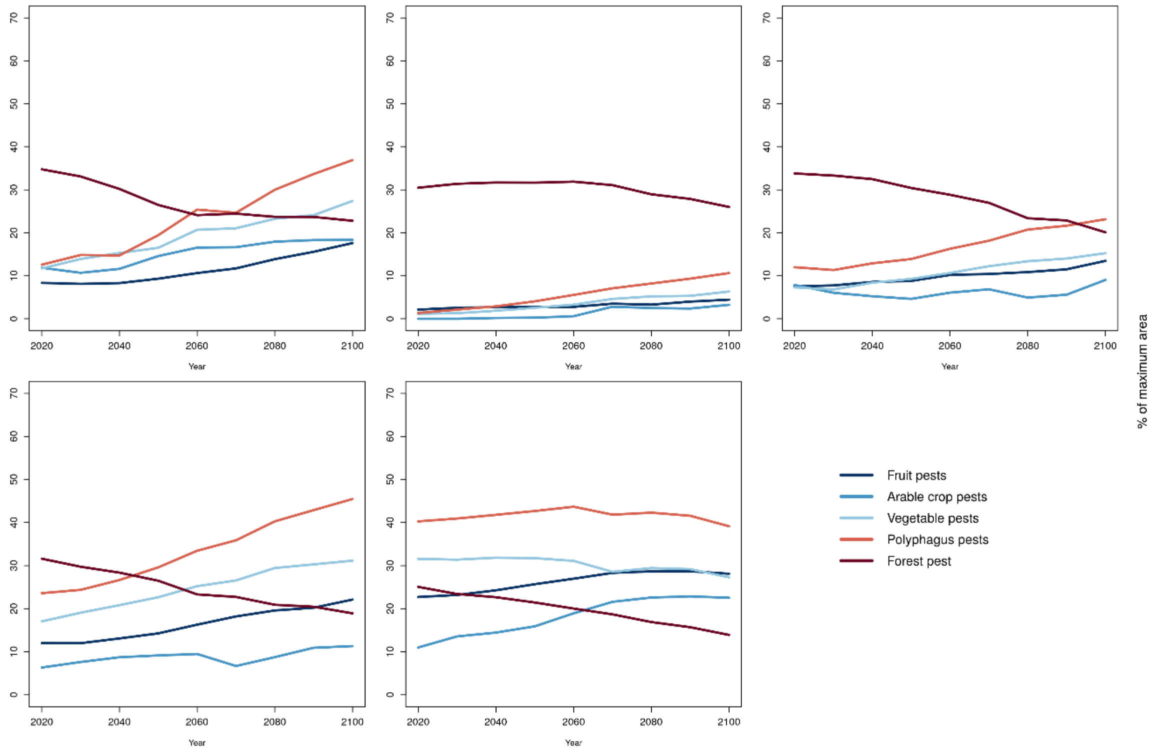
Supplementary Figure 6: Same as Fig. 3 but for modularity and specialisation. Modularity was calculated with the calculateModule function (R package bipartite 2.11). For specialization, we calculated the sum of all links for each pest species and used the mean of all sums as a metric.



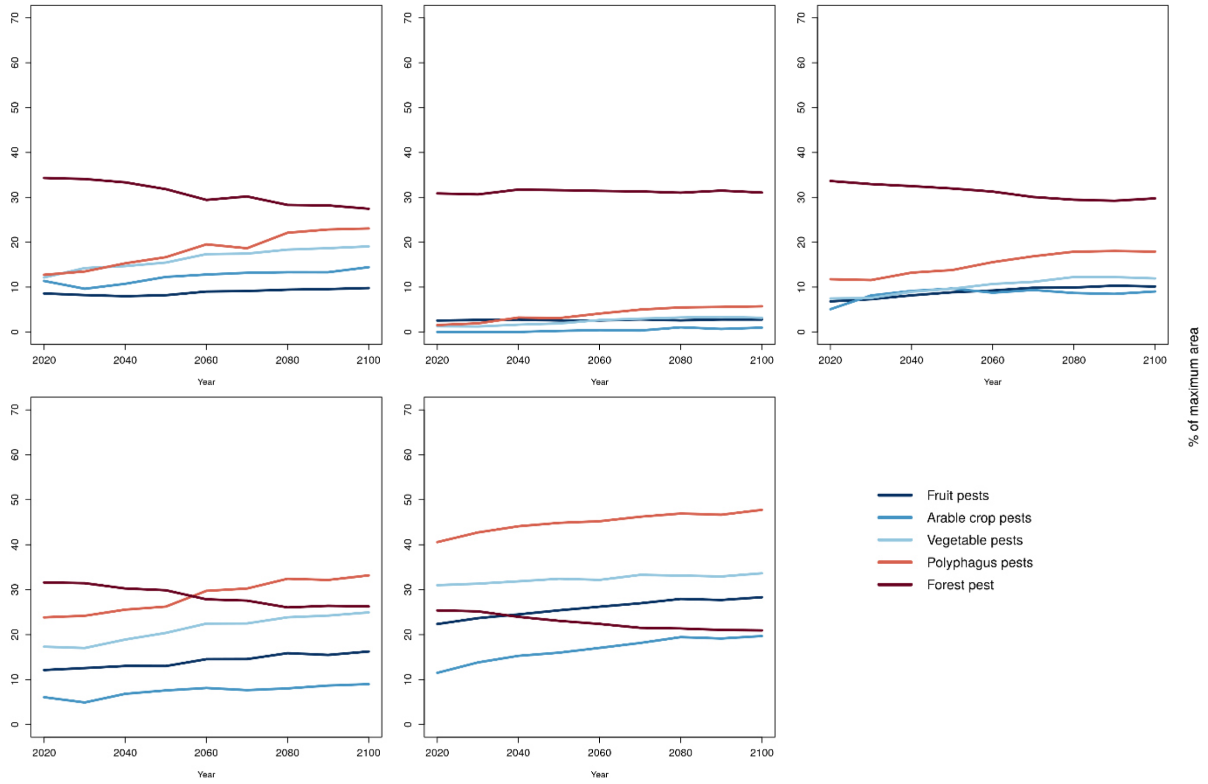
Supplementary Figure 7: Change in the area of overlap over time for the five different host categories under the RCP8.5 scenario. Panels from left top to right bottom: British Isles, Northern Europe, Eastern Europe, Western Europe, Southern Europe.



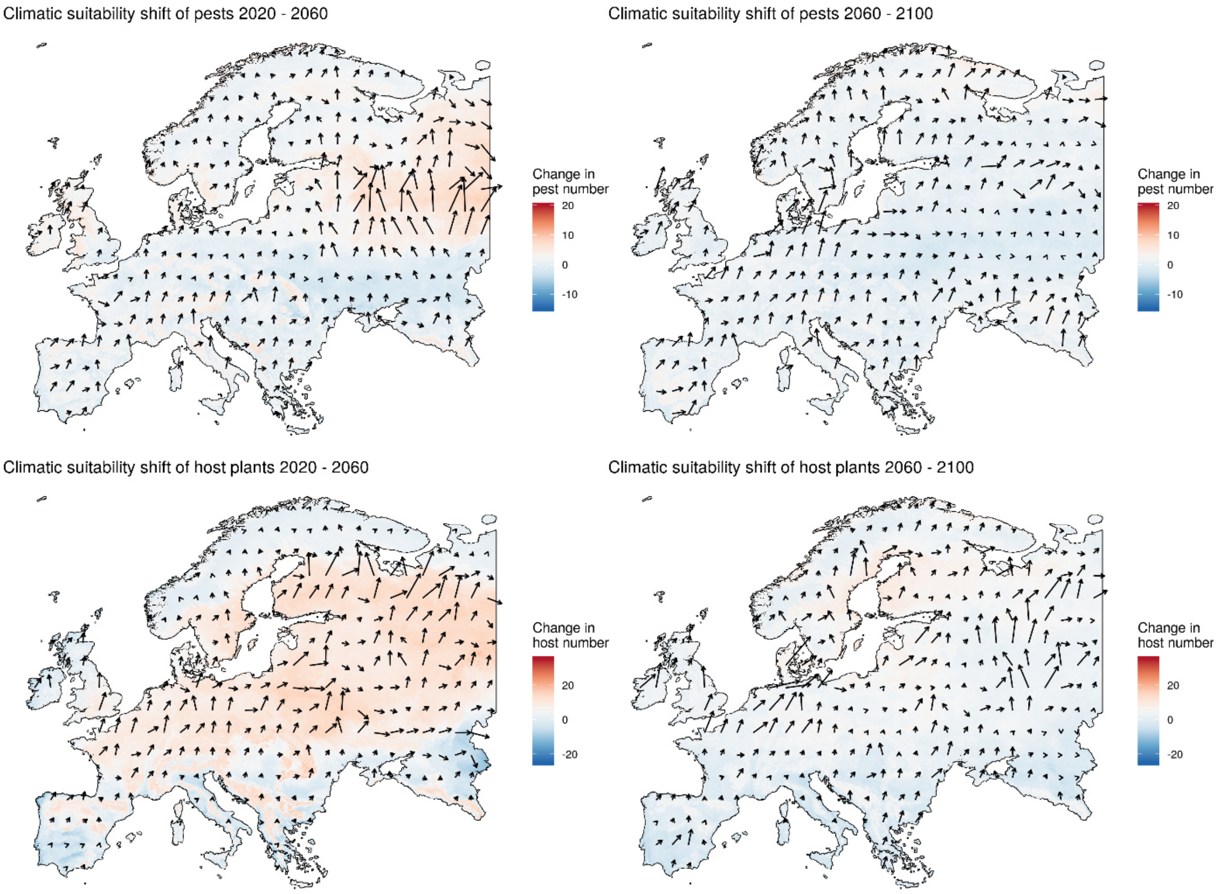
Supplementary Figure 8: Same as fig. S7 but under RCP4.5 scenario.



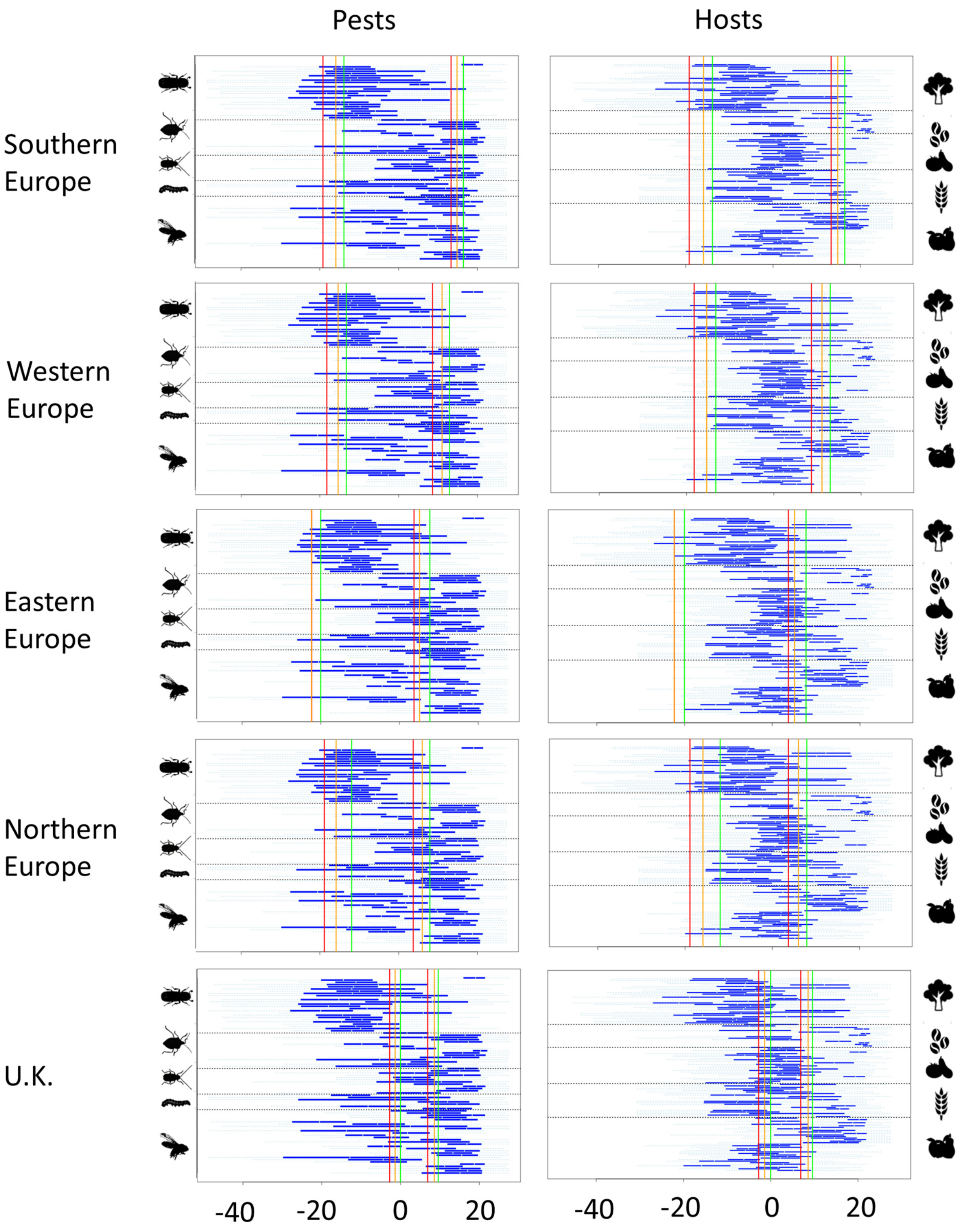
Supplementary Figure 9: Change in the area of overlap over time for the five different pest categories under the RCP8.5 scenario. Panels from left top to right bottom: British Isles, Northern Europe, Eastern Europe, Western Europe, Southern Europe.



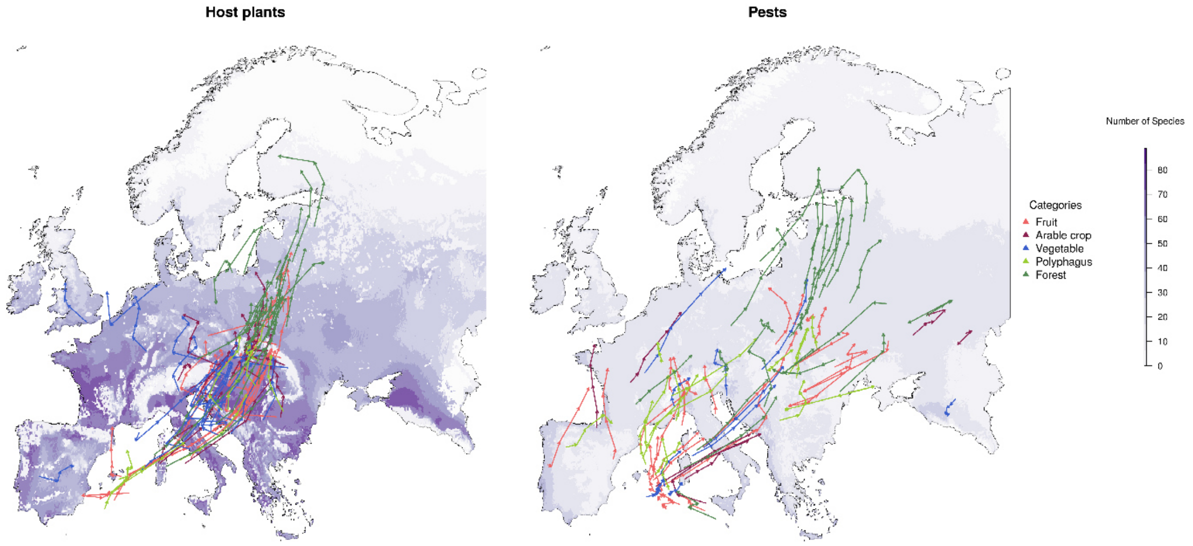
Supplementary Figure 10: Same as fig. S9 but under RCP4.5 scenario.



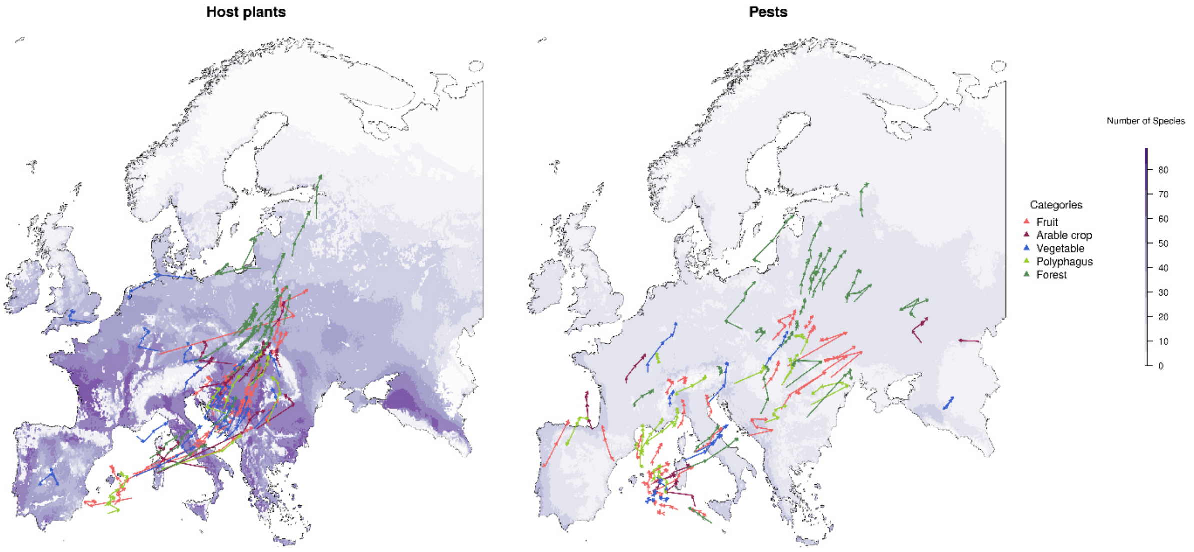
Supplementary Figure 11: Movement patterns of pests and host plants, same as figure 4 but for RCP4.5.



Supplementary Figure 12: Niche distribution of pests (left) and host plants (right) over Min Temp. Blue boxes show the niche of each pest. Vertical lines show the border of Min Temp conditions in Europe (red for 2020, orange for 2060 and green for 2100). Dashed horizontal lines are borders of pest categories. From bottom to top: fruit pests, arable crop pests, vegetable pests, polyphagous pests, forest pests.



Supplementary Figure 13: Centroid shift between 2020 and 2100 in four time steps (2020 – 2040, 2040 – 2060, 2060 – 2080, 2080 – 2100) for the five different categories of host plants (left) and pests (right). Centroids were calculated on the individual distribution maps under the RCP8.5 scenario.



Supplementary Figure 14: Same as figure S12 but for RCP4.5.

Supplementary tables

Supplementary Table 1: List of pest species. Categories: 1 = Fruit pests, 2 = Arabale crop pests, 3 = Vegetable pests, 4 = Polyphagous pests, 5 = Forest pests.

Species	Order	Cat	Variable 1	Variable 2	Variable 3	Variable 4
Acleris variana	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Agrilus anxius	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Agrilus planipennis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Aleurocanthus spiniferus	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Aleurocanthus woglumi	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Anastrepha fraterculus	Diptera	1	GDD	Temp season	NA	NA
Anastrepha ludens	Diptera	1	Min Temp	GDD	An precip	Precip season
Anastrepha obliqua	Diptera	1	GDD	Temp season	NA	NA
Anoplophora glabripennis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Anthonomus bisignifer	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Anthonomus grandis	Coleoptera	2	Min Temp	GDD	An precip	Precip season
Anthonomus quadrigibbus	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Anthonomus signatus	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Bactericera cockerelli	Hemiptera	3	Min Temp	GDD	An precip	Precip season
Bactrocera cucumis	Diptera	3	Min Temp	GDD	An precip	Precip season
Bactrocera cucurbitae	Diptera	3	GDD	An precip	NA	NA
Bactrocera invadens	Diptera	1	GDD	An precip	NA	NA
Bactrocera latifrons	Diptera	3	Min Temp	GDD	An precip	Precip season
Bactrocera tryoni	Diptera	1	Min Temp	GDD	An precip	Precip season
Bactrocera zonata	Diptera	1	Min Temp	GDD	An precip	Precip season
Ceratitis rosa	Diptera	1	GDD	An precip	NA	NA
Choristoneura conflictana	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Choristoneura occidentalis	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Choristoneura rosaceana	Lepidoptera	4	Min Temp	GDD	An precip	Precip season
Conotrachelus nenuphar	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Dacus ciliatus	Diptera	3	GDD	An precip	NA	NA
Dendroctonus adjunctus	Coleoptera	5	GDD	An precip	NA	NA
Dendroctonus brevicomis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Dendroctonus frontalis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Dendroctonus ponderosae	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Dendroctonus pseudotsugae	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Dendroctonus rufipennis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Dendrolimus superans	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Diabrotica barberi	Coleoptera	2	Min Temp	GDD	An precip	Precip season
Diabrotica speciosa	Coleoptera	2	GDD	An precip	Temp season	NA
Diabrotica undecimpunctata howardi	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Diabrotica undecimpunctata undecimpunctata	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Diaphorina citri	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Epitrix cucumeris	Coleoptera	3	Min Temp	GDD	An precip	Precip season
Epitrix subcrinita	Coleoptera	3	Min Temp	GDD	An precip	Precip season
Euwallacea fornicatus	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Gnathotrichus sulcatus	Coleoptera	5	GDD	An precip	NA	NA

Gonipterus scutellatus	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Grapholita packardi	Lepidoptera	1	Min Temp	GDD	An precip	Precip season
Helicoverpa zea	Lepidoptera	4	Min Temp	GDD	An precip	Precip season
Heteronychus arator	Coleoptera	3	GDD	An precip	NA	NA
Homalodisca vitripennis	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Ips calligraphus	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Ips grandicollis	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Ips pini	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Leucinodes orbonalis	Lepidoptera	3	Min Temp	GDD	An precip	Precip season
Limonius californicus	Coleoptera	3	Min Temp	GDD	An precip	Precip season
Liriomyza sativae	Diptera	4	Min Temp	GDD	An precip	Precip season
Listronotus bonariensis	Coleoptera	2	Min Temp	GDD	An precip	Precip season
Lycorma delicatula	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Lymantria mathura	Lepidoptera	4	Min Temp	GDD	An precip	Precip season
Maconellicoccus hirsutus	Hemiptera	4	Min Temp	GDD	An precip	Precip season
Malacosoma americanum	Lepidoptera	1	Min Temp	GDD	An precip	Precip season
Malacosoma disstria	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Massicus raddei	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Megacopta cribraria	Hemiptera	2	Min Temp	GDD	An precip	Precip season
Melanotus communis	Coleoptera	3	Min Temp	GDD	An precip	Precip season
Metamasius hemipterus	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Naupactus leucoloma	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Naupactus xanthographus	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Neodiprion abietis	Hymenoptera	5	Min Temp	GDD	An precip	Precip season
Oemona hirta	Coleoptera	4	GDD	An precip	NA	NA
Orgyia pseudotsugata	Lepidoptera	5	Min Temp	GDD	An precip	Precip season
Pissodes strobi	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Platynota stultana	Lepidoptera	2	Min Temp	GDD	An precip	Precip season
Polygraphus proximus	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Popilia japonica	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Pseudacysta perseae	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Rhagoletis mendax	Diptera	1	Min Temp	GDD	An precip	Precip season
Rhagoletis pomonella	Diptera	1	Min Temp	GDD	An precip	Precip season
Rhynchophorus palmarum	Coleoptera	5	Min Temp	GDD	An precip	Precip season
Saperda candida	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Scirtothrips dorsalis	Thysanoptera	4	Min Temp	GDD	An precip	Precip season
Spodoptera eridania	Lepidoptera	4	GDD	An precip	NA	NA
Spodoptera frugiperda	Lepidoptera	4	Min Temp	GDD	An precip	Precip season
Spodoptera litura	Lepidoptera	4	Min Temp	GDD	An precip	Precip season
Strauzia longipennis	Diptera	2	Min Temp	GDD	An precip	Precip season
Tecia solanivora	Lepidoptera	3	GDD	An precip	Temp season	NA
Thaumatotibia leucotreta	Lepidoptera	1	Min Temp	GDD	An precip	Precip season
Trioza erytreae	Hemiptera	1	Min Temp	GDD	An precip	Precip season
Xylosandrus compactus	Coleoptera	1	Min Temp	GDD	An precip	Precip season
Xylosandrus crassiusculus	Coleoptera	4	Min Temp	GDD	An precip	Precip season
Zaprionus indianus	Diptera	1	GDD	An precip	NA	NA
Zaprionus tuberculatus	Diptera	1	GDD	An precip	NA	NA

Supplementary Table 2: List of host plant species. Categories: 1 = Fruit crops, 2 = Arabale crops, 3 = Vegetables, 4 = Other crops, 5 = Forest trees

Species	Category	Variable 1	Variable 2
almond	1	Min Temp	GDD
apple	1	Min Temp	GDD
apricot	1	Min Temp	GDD
blueberry	1	Min Temp	GDD
carob	1	Min Temp	GDD
cherry	1	Min Temp	GDD
cranberry	1	Min Temp	GDD
gooseberry	1	Min Temp	GDD
grape	1	Min Temp	GDD
kiwi	1	Min Temp	GDD
peachetc	1	Min Temp	GDD
pear	1	Min Temp	GDD
plum	1	Min Temp	GDD
rasberry	1	Min Temp	GDD
sourcherry	1	Min Temp	GDD
strawberry	1	Min Temp	GDD
tangetc	1	Min Temp	GDD
fig	1	Min Temp	GDD
avocado	1	Min Temp	GDD
cashew	1	Min Temp	GDD
citrusnes	1	Min Temp	GDD
date	1	Min Temp	GDD
grapefruitetc	1	Min Temp	GDD
groundnut	1	Min Temp	GDD
karite	1	Min Temp	GDD
lemonlime	1	Min Temp	GDD
mango	1	Min Temp	GDD
olive	1	Min Temp	GDD
orange	1	Min Temp	GDD
papaya	1	Min Temp	GDD
persimmon	1	Min Temp	GDD
pineapple	1	Min Temp	GDD
pistachio	1	Min Temp	GDD
plantain	1	Min Temp	GDD
quince	1	Min Temp	GDD
areca	2	Min Temp	GDD
barley	2	Min Temp	GDD
bean	2	Min Temp	GDD
broadbean	2	Min Temp	GDD
buckwheat	2	Min Temp	GDD
castor	2	Min Temp	GDD
chickpea	2	Min Temp	GDD
cowpea	2	Min Temp	GDD
maize	2	Min Temp	GDD
oats	2	Min Temp	GDD
pea	2	Min Temp	GDD

pigeonpea	2	Min Temp	GDD
rapeseed	2	Min Temp	GDD
rice	2	Min Temp	GDD
rye	2	Min Temp	GDD
sorghum	2	Min Temp	GDD
soybean	2	Min Temp	GDD
triticale	2	Min Temp	GDD
wheat	2	Min Temp	GDD
alfalfa	3	Min Temp	GDD
beetfor	3	Min Temp	GDD
cabbage	3	Min Temp	GDD
carrot	3	Min Temp	GDD
cassava	3	Min Temp	GDD
cauliflower	3	Min Temp	GDD
chilleetc	3	Min Temp	GDD
clover	3	Min Temp	GDD
cucumberetc	3	Min Temp	GDD
eggplant	3	Min Temp	GDD
grassnes	3	Min Temp	GDD
greenbean	2	Min Temp	GDD
greencorn	2	Min Temp	GDD
greenpea	2	Min Temp	GDD
lettuce	3	Min Temp	GDD
melonetc	3	Min Temp	GDD
okra	3	Min Temp	GDD
onion	3	Min Temp	GDD
potato	3	Min Temp	GDD
pumpkinetc	3	Min Temp	GDD
spinach	3	Min Temp	GDD
swedefor	3	Min Temp	GDD
sweetpotato	3	Min Temp	GDD
taro	3	Min Temp	GDD
tomato	3	Min Temp	GDD
turnipfor	3	Min Temp	GDD
watermelon	3	Min Temp	GDD
cinnamon	4	Min Temp	GDD
cocoa	4	Min Temp	GDD
coconut	4	Min Temp	GDD
coffee	4	Min Temp	GDD
cotton	4	Min Temp	GDD
flax	4	Min Temp	GDD
hemp	4	Min Temp	GDD
kapokseed	4	Min Temp	GDD
oilpalm	4	Min Temp	GDD
pimento	4	Min Temp	GDD
ramie	4	Min Temp	GDD
rubber	4	Min Temp	GDD
sugarcane	4	Min Temp	GDD
sunflower	4	Min Temp	GDD
tobacco	4	Min Temp	GDD
Abies alba	5	An precip	GDD

Acer campestre	5	An precip	GDD
Acer platanoides	5	An precip	GDD
Acer pseudoplatanus	5	An precip	GDD
Alnus glutinosa	5	An precip	GDD
Betula pendula	5	An precip	GDD
Castanea sativa	5	An precip	GDD
Corylus avellana	5	An precip	GDD
Eucalyptus globulus	5	An precip	GDD
Fagus sylvatica	5	An precip	GDD
Fraxinus excelsior	5	An precip	GDD
Juglans regia	5	An precip	GDD
Larix decidua	5	An precip	GDD
Picea abies	5	An precip	GDD
Pinus nigra	5	An precip	GDD
Pinus pinaster	5	An precip	GDD
Pinus pinea	5	An precip	GDD
Pinus sylvestris	5	An precip	GDD
Populus alba	5	An precip	GDD
Populus nigra	5	An precip	GDD
Populus tremula	5	An precip	GDD
Prunus avium	5	An precip	GDD
Pseudotsuga menziesii	5	An precip	GDD
Quercus petraea	5	An precip	GDD
Quercus robur	5	An precip	GDD
Quercus suber	5	An precip	GDD
Robinia pseudoacacia	5	An precip	GDD
Salix alba	5	An precip	GDD
Tilia cordata	5	An precip	GDD
Ulmus laevis	5	An precip	GDD

Supplementary Table 3: Pest evaluation metrics: AUC scores and TSS values of the ensemble of each species and average of all GCMs and RCPs.

Species name	AUC	TSS	tss.threshold
Acleris variana	0.8009	0.5605	0.3307
Agrilus anxius	0.8535	0.6377	0.3962
Agrilus planipennis	0.959	0.8118	0.5347
Aleurocanthus spiniferus	0.8887	0.7315	0.386
Aleurocanthus woglumi	0.9124	0.7883	0.3656
Anastrepha ludens	0.8677	0.6808	0.4299
Anoplophora glabripennis	0.8783	0.6562	0.4054
Anthonomus bisignifer	0.9737	0.9129	0.377
Anthonomus grandis	0.8904	0.6899	0.402
Anthonomus quadrigibbus	0.7682	0.4983	0.3979
Anthonomus signatus	0.7912	0.6034	0.4516
Bactericera cockerelli	0.9255	0.7254	0.478
Bactrocera cucumis	0.9249	0.7757	0.4612
Bactrocera latifrons	0.8174	0.5482	0.436
Bactrocera tryoni	0.9302	0.7687	0.5479
Bactrocera zonata	0.8493	0.5571	0.4596
Choristoneura conflictana	0.8087	0.5833	0.3609
Choristoneura occidentalis	0.8832	0.6679	0.463
Choristoneura rosaceana	0.8879	0.6393	0.4176
Conotrachelus nenuphar	0.859	0.6467	0.3586
Dendroctonus brevicomis	0.8823	0.6885	0.4099
Dendroctonus frontalis	0.89	0.7075	0.3694
Dendroctonus ponderosae	0.7966	0.499	0.4323
Dendroctonus pseudotsugae	0.8363	0.5779	0.4242
Dendroctonus rufipennis	0.8442	0.5657	0.4356
Dendrolimus superans	0.8973	0.7921	0.4996
Diabrotica barberi	0.9824	0.9121	0.3881
Diabrotica undecimpunctata howardi	0.8505	0.599	0.3981
Diabrotica undecimpunctata undecimpunctata	0.9766	0.8907	0.4419
Diaphorina citri	0.8584	0.6093	0.4361
Epitrix cucumeris	0.9052	0.7346	0.4392
Epitrix subcrinita	0.9608	0.848	0.428
Euwallacea fornicatus	0.8042	0.6321	0.4829
Gonipterus scutellatus	0.8985	0.7028	0.4125
Grapholita packardi	0.8936	0.7149	0.4467
Helicoverpa zea	0.8702	0.5821	0.4816
Homalodisca vitripennis	0.9713	0.8453	0.4206
Ips calligraphus	0.7984	0.5481	0.4888
Ips grandicollis	0.9177	0.7105	0.4496
Ips pini	0.8989	0.6819	0.5206
Leucinodes orbonalis	0.9097	0.7505	0.5007
Limonius californicus	0.8326	0.5638	0.4392
Liriomyza sativae	0.8988	0.6747	0.4077

Listronotus bonariensis	0.8877	0.7082	0.3901
Lycorma delicatula	0.9666	0.8468	0.3582
Lymantria mathura	0.9381	0.7945	0.44
Maconellicoccus hirsutus	0.9388	0.7754	0.3846
Malacosoma americanum	0.9725	0.8425	0.6019
Malacosoma disstria	0.9462	0.75	0.5034
Massicus raddei	0.9281	0.8768	0.5304
Megacopta cribraria	0.9843	0.9221	0.4146
Melanotus communis	0.8533	0.6871	0.4449
Metamasius hemipterus	0.9937	0.9545	0.4083
Naupactus leucoloma	0.9263	0.7265	0.4179
Naupactus xanthographus	0.9322	0.7718	0.4723
Neodiprion abietis	0.9229	0.7877	0.3857
Orgyia pseudotsugata	0.7699	0.5643	0.3768
Pissodes strobi	0.8304	0.6493	0.3558
Platynota stultana	0.9607	0.8794	0.5311
Polygraphus proximus	0.9809	0.9236	0.4528
Popilia japonica	0.9773	0.8585	0.5781
Pseudacysta perseae	0.9263	0.7942	0.4091
Rhagoletis mendax	0.8488	0.6429	0.4137
Rhagoletis pomonella	0.9195	0.7233	0.4141
Rhynchophorus palmarum	0.9717	0.8825	0.3985
Saperda candida	0.8577	0.6631	0.4414
Scirtothrips dorsalis	0.786	0.5174	0.3705
Spodoptera frugiperda	0.8917	0.6621	0.4795
Spodoptera litura	0.9135	0.7054	0.5139
Strauzia longipennis	0.866	0.6499	0.4057
Thaumatotibia leucotreta	0.905	0.7377	0.3684
Trioza erytreae	0.9284	0.784	0.416
Xylosandrus compactus	0.9607	0.8687	0.498
Xylosandrus crassiusculus	0.886	0.6758	0.4881
Anastrepha fraterculus	0.7829	0.4472	0.4493
Anastrepha obliqua	0.7263	0.3435	0.4555
Bactrocera invadens	0.7962	0.4672	0.4793
Ceratitis rosa	0.8458	0.54	0.4835
Dacus ciliatus	0.8287	0.5295	0.4757
Diabrotica speciosa	0.8051	0.5333	0.5333
Gnathotrichus sulcatus	0.7851	0.4825	0.4061
Heteronychus arator	0.9425	0.8274	0.418
Oemona hirta	0.9361	0.8192	0.496
Spodoptera eridania	0.8251	0.6246	0.3625
Tecia solanivora	0.9694	0.9087	0.415
Bactrocera cucurbitae	0.8335	0.5694	0.419
Dendroctonus adjunctus	0.7264	0.4053	0.3989
Zaprionus tuberculatus	0.7311	0.4425	0.3991
Zaprionus indianus	0.8133	0.5389	0.4392

Supplementary Table 4: Host evaluation metrics: AUC scores and TSS values of the ensemble of each species and average of all GCMs and RCPs.

Species name	**AUC**	**TSS**	**tss.threshold**
almond	0.9291	0.7611	0.5451
apple	0.8828	0.5979	0.5503
apricot	0.8483	0.5454	0.5076
blueberry	0.8881	0.6556	0.5673
carob	0.9227	0.7268	0.5467
cherry	0.8437	0.5492	0.5266
cranberry	0.9733	0.8911	0.6226
gooseberry	0.9392	0.7915	0.4983
grape	0.8938	0.6564	0.5425
kiwi	0.8742	0.6504	0.553
peachetc	0.8639	0.5998	0.5306
pear	0.8836	0.6094	0.5779
plum	0.8563	0.5903	0.4539
rasberry	0.9197	0.7147	0.553
sourcherry	0.9333	0.7456	0.5799
strawberry	0.8822	0.6561	0.5653
tangetc	0.8033	0.4769	0.5587
fig	0.8556	0.5845	0.5772
avocado	0.8431	0.5828	0.4794
cashew	0.7784	0.449	0.4969
citrusnes	0.815	0.536	0.5589
date	0.8724	0.603	0.5114
grapefruitetc	0.8653	0.5636	0.5493
groundnut	0.8212	0.5143	0.5188
karite	0.8295	0.5666	0.5074
lemonlime	0.8047	0.4811	0.5496
mango	0.8171	0.4927	0.5663
olive	0.9352	0.7516	0.5485
orange	0.8673	0.6053	0.5353
papaya	0.8127	0.4782	0.5343
persimmon	0.8869	0.6183	0.4864
pineapple	0.7534	0.3707	0.5132
pistachio	0.8864	0.6568	0.5697
plantain	0.8018	0.4828	0.4836
quince	0.8674	0.6204	0.5843
areca	0.7822	0.4615	0.4727
barley	0.891	0.6567	0.5082
bean	0.7407	0.3617	0.4765
broadbean	0.8056	0.5021	0.5563
buckwheat	0.8378	0.5625	0.5036
castor	0.9282	0.7145	0.4904

chickpea	0.8225	0.5076	0.447
cowpea	0.8659	0.5851	0.5869
maize	0.8489	0.5802	0.5042
oats	0.8709	0.6434	0.5126
pea	0.8697	0.6166	0.4521
pigeonpea	0.8617	0.5791	0.5707
rapeseed	0.8556	0.6071	0.4733
rice	0.7901	0.4548	0.5469
rye	0.9281	0.7368	0.5923
sorghum	0.8143	0.4683	0.5284
soybean	0.8417	0.5255	0.5229
triticale	0.909	0.7022	0.5739
wheat	0.8113	0.4874	0.4897
alfalfa	0.8373	0.5539	0.5094
beetfor	0.8822	0.6521	0.4569
cabbage	0.8804	0.6097	0.5397
carrot	0.8431	0.5678	0.5116
cassava	0.7212	0.3409	0.5315
cauliflower	0.8816	0.6613	0.5976
chilleetc	0.8549	0.5796	0.5141
clover	0.9293	0.7441	0.5424
cucumberetc	0.8344	0.5212	0.4986
eggplant	0.8141	0.5183	0.5403
grassnes	0.8993	0.6626	0.5429
greenbean	0.795	0.4711	0.4922
greencorn	0.8092	0.4823	0.5734
greenpea	0.7931	0.4325	0.4921
lettuce	0.8836	0.6554	0.5099
melonetc	0.8221	0.5239	0.5182
okra	0.8392	0.5488	0.5078
onion	0.8017	0.4604	0.5116
potato	0.831	0.5112	0.491
pumpkinetc	0.77	0.4017	0.5407
spinach	0.868	0.6001	0.4903
swedefor	0.952	0.8535	0.5777
sweetpotato	0.8524	0.5524	0.5134
taro	0.8543	0.5921	0.5196
tomato	0.8254	0.5264	0.5317
turnipfor	0.9278	0.8009	0.628
watermelon	0.8661	0.5903	0.4994
cinnamon	0.8796	0.6302	0.5176
cocoa	0.8311	0.5108	0.5666
coconut	0.8417	0.5267	0.5204
coffee	0.8323	0.5424	0.4703
cotton	0.8323	0.5036	0.5068
flax	0.8139	0.5198	0.5019

hemp	0.8232	0.5288	0.5454
kapokseed	0.8192	0.5386	0.3957
oilpalm	0.8787	0.5976	0.5056
pimento	0.7671	0.3985	0.4918
ramie	0.8116	0.5341	0.5228
rubber	0.8263	0.5111	0.5192
sugarcane	0.8036	0.4483	0.535
sunflower	0.8731	0.6087	0.561
tobacco	0.8415	0.532	0.5034
Abies alba	0.8266	0.5003	0.5136
Acer campestre	0.8665	0.6407	0.5361
Acer platanoides	0.7991	0.5265	0.4749
Acer pseudoplatanus	0.7878	0.474	0.4721
Alnus glutinosa	0.8347	0.5812	0.4631
Betula pendula	0.7237	0.3835	0.4264
Castanea sativa	0.9307	0.7639	0.5176
Corylus avellana	0.8795	0.6388	0.446
Eucalyptus globulus	0.9531	0.812	0.5011
Fagus sylvatica	0.8575	0.6018	0.4299
Fraxinus excelsior	0.8648	0.6664	0.4527
Juglans regia	0.9413	0.7682	0.5156
Larix decidua	0.8811	0.6008	0.5109
Picea abies	0.7593	0.4346	0.489
Pinus nigra	0.7466	0.3877	0.5004
Pinus pinaster	0.8722	0.5906	0.47
Pinus pinea	0.9209	0.7314	0.4678
Pinus sylvestris	0.786	0.4906	0.4551
Populus alba	0.7556	0.4332	0.4823
Populus nigra	0.7877	0.5002	0.4889
Populus tremula	0.8113	0.5243	0.4902
Prunus avium	0.9123	0.7319	0.4486
Pseudotsuga menziesii	0.8801	0.6455	0.5606
Quercus petraea	0.9161	0.7508	0.4724
Quercus robur	0.8853	0.6989	0.4148
Quercus suber	0.9167	0.7267	0.4797
Robinia pseudoacacia	0.9053	0.6709	0.5956
Salix alba	0.9097	0.6868	0.5417
Tilia cordata	0.8494	0.6235	0.5022
Ulmus laevis	0.8526	0.6265	0.5073

Supplementary Table 5: Area with suitable climatic habitat of all host plants under RCP8.5.

Species name	**2020**	**2100**	**change**	**change in %**
almond	1032408.07	4000516.28	2968108.21	293.751729
apple	3254431.37	4257849.09	1003417.72	31.0394461
apricot	2342347.98	5299097.64	2956749.66	126.823638
blueberry	3525838.97	480630.156	-3045208.8	-87.175005
carob	1742656.4	4667254.17	2924597.77	167.759557
cherry	3814216.46	3771293.94	-42922.523	0.45703138
cranberry	627159.497	230315.215	-396844.28	-41.989644
gooseberry	4399173.16	2027781.7	-2371391.5	-53.721071
grape	2117999.18	5072976.89	2954977.71	140.847296
kiwi	2785289.85	4776420.56	1991130.71	109.915061
peachetc	2360522.47	4243017.65	1882495.18	82.9495409
pear	1404409.18	2907795.85	1503386.67	104.573722
plum	3164038.43	4374252.36	1210213.93	38.034578
rasberry	3840614.97	2425054.57	-1415560.4	-36.935591
sourcherry	3759434.8	2691685.84	-1067749	-28.166283
strawberry	2935115.16	3063824.64	128709.475	8.6546808
tangetc	2899457.14	4746209.19	1846752.05	65.5299122
fig	2083935.04	5154998.35	3071063.31	148.981288
avocado	465484.892	2561016.82	2095531.93	472.406533
cashew	0	3196.95732	3196.95732	NA
citrusnes	0	1644.59491	1644.59491	NA
date	102378.955	152628.116	50249.161	48.734971
grapefruitetc	92174.3665	842567.555	750393.188	1074.16263
groundnut	481038.689	2351871.31	1870832.63	436.534163
karite	0	0	0	NA
lemonlime	358290.294	745684.187	387393.894	126.315463
mango	0	7121.55421	7121.55421	Inf
olive	883921.454	3704732.46	2820811.01	319.609949
orange	209649.8	1265377	1055727.2	545.758296
papaya	49028.8219	133.786999	-48895.035	-99.705848
persimmon	2043955.47	4327522.15	2283566.68	110.568605
pineapple	756.998354	829.242054	72.2436991	NA
pistachio	443665.803	2026242.57	1582576.76	353.336576
plantain	5613399.03	5615324.84	1925.80465	0.03434248
quince	2194102.08	3608384.59	1414282.52	64.6968248
areca	1395866.63	2001903.03	606036.398	934.654187
barley	5487322.96	3856374.86	-1630948.1	-29.638863
bean	3790633.82	4527342.68	736708.856	20.1068616
broadbean	5136263.22	4559991.76	-576271.47	-10.779358
buckwheat	4164889.72	4324321.79	159432.071	3.95250488
castor	0	0	0	NA
chickpea	406918.253	88460.6274	-318457.63	Inf
cowpea	0	0	0	NA
maize	4992465.1	4318892.54	-673572.56	-13.23313
oats	5468277.8	3066210.59	-2402067.2	-43.975787
pea	5362412.42	3739453.07	-1622959.3	-30.123327
pigeonpea	0	18791.8831	18791.8831	Inf

rapeseed	2991882.92	3200704.7	208821.778	6.13920335
rice	631263.607	2496404.62	1865141.01	283.078963
rye	3774543.31	912503.706	-2862039.6	-75.998295
sorghum	518294.2	2757769.2	2239475	479.840802
soybean	1446633.93	4301807.96	2855174.03	197.487267
triticale	3969335.04	1963572.03	-2005763	-50.62388
wheat	5338827.86	4881246.25	-457581.61	-8.5182259
greenbean	3163911.19	4282194.66	1118283.47	41.1522969
greencorn	3395222.38	2897705.87	-497516.51	-12.362191
greenpea	2904564.25	3547577.09	643012.842	22.944007
alfalfa	4139848.27	4491963.13	352114.854	9.84173378
beetfor	1624857.26	717533.172	-907324.08	-55.75436
cabbage	1478942.46	3781500.83	2302558.37	157.767757
carrot	4209533.81	4460270.12	250736.314	6.1328124
cassava	3839.80272	2677.12849	-1162.6742	135.819435
cauliflower	511607.139	2362897.09	1851289.96	353.62449
chilleetc	2158286.46	4047356.09	1889069.62	89.2725041
clover	2439721.96	1499349.44	-940372.52	-39.794485
cucumberetc	2050501.39	4259275.31	2208773.92	107.012327
eggplant	1059460.06	3105879.59	2046419.53	195.879232
grassnes	2838740.6	2660485.53	-178255.06	-3.4614892
lettuce	1295692.67	2312812.67	1017120	82.9838183
melonetc	2110056.91	4011397.53	1901340.63	90.2884075
okra	0	18503.0539	18503.0539	Inf
onion	2912561.02	4228476.04	1315915.02	48.0266479
potato	5294226.9	4229209.98	-1065016.9	-19.889347
pumpkinetc	2053599.62	3907137.24	1853537.62	86.8545631
spinach	1638084.79	4202618.74	2564533.96	155.548539
swedefor	481069.331	48163.3112	-432906.02	-91.01766
sweetpotato	1834246.74	5161476.46	3327229.72	181.977798
taro	1799.19487	9430.87683	7631.68197	417.208163
tomato	2806672.79	4028381.72	1221708.93	44.3833547
turnipfor	430496.655	142689.2	-287807.45	-65.244387
watermelon	1491868.28	4660723.92	3168855.64	211.668417
cinnamon	29.822491	127.215108	97.3926175	NA
cocoa	0	1017.30682	1017.30682	NA
coconut	0	598.77051	598.77051	NA
coffee	51992.97	155256.22	103263.25	247.172385
cotton	359196.026	2742743.65	2383547.62	697.475698
flax	5163731.71	4533971.14	-629760.57	-12.243186
hemp	2513349.45	3790367.59	1277018.14	52.795279
kapokseed	977.971089	0	-977.97109	-100
oilpalm	0	189.693927	189.693927	NA
pimento	183152.264	1445073.81	1261921.54	734.411259
ramie	1792442.6	5272141.66	3479699.05	195.33548
rubber	0	0	0	NA
sugarcane	27787.8788	627015.968	599228.09	3747.26585
sunflower	3470541.57	3746681.87	276140.292	10.613495
tobacco	2612044.49	4007455.38	1395410.9	54.8536923
Abies alba	1271989.58	326329.85	-945659.73	-72.947618
Acer campestre	7017142.64	7425246.26	408103.614	5.9161451

Acer platanoides	5614096.14	5108623.84	-505472.3	-8.9475111
Acer pseudoplatanus	3688017.19	3193738.24	-494278.94	-12.806784
Alnus glutinosa	5169549.65	5691394.38	521844.73	10.0752586
Betula pendula	5259409.84	2750962.97	-2508446.9	-47.607361
Castanea sativa	3300893.93	5394369.75	2093475.82	63.6746686
Corylus avellana	4598058.85	4101699.33	-496359.52	-10.783591
Eucalyptus globulus	621525.039	2451903.37	1830378.33	298.758654
Fagus sylvatica	4053818.14	3552331.2	-501486.94	-12.610831
Fraxinus excelsior	6153831.79	6259737.03	105905.24	1.69774433
Juglans regia	5067588.26	5946602.33	879014.077	17.375463
Larix decidua	755532.775	167251.248	-588281.53	-77.80547
Picea abies	3431528.58	790049.61	-2641479	-77.156949
Pinus nigra	3594491.46	5155629.51	1561138.05	44.3395886
Pinus pinaster	1898928.16	4613178.84	2714250.68	142.911838
Pinus pinea	686961.674	2945673.25	2258711.58	328.534287
Pinus sylvestris	4650755.21	1418925.29	-3231829.9	-69.520825
Populus alba	4283613.4	7441974.08	3158360.68	73.7436181
Populus nigra	6817675.51	8124045.84	1306370.33	19.1983868
Populus tremula	7009383.7	4883827.97	-2125555.7	-30.382759
Prunus avium	5472761.08	6013285.53	540524.456	9.86227798
Pseudotsuga menziesii	3971050.13	3143780.2	-827269.93	-20.984379
Quercus petraea	5102275.26	6018105.57	915830.308	17.9370936
Quercus robur	5858345.59	5511073.17	-347272.42	-5.9151801
Quercus suber	1037210.77	4378159.8	3340949.04	320.424422
Robinia pseudoacacia	3736400.64	4334947.19	598546.546	16.3041782
Salix alba	4415357.67	4870576.64	455218.972	10.2764455
Tilia cordata	6166294.63	5029658.92	-1136635.7	-18.292572
Ulmus laevis	5812747.51	4305493.79	-1507253.7	-25.74863

Supplementary Table 6: Same as table S5 but for RCP4.5

Species name	2020	2100	change	change in %
almond	995735.491	1974709.03	978973.54	99.4702786
apple	3062689.63	4537806.9	1475117.27	48.810419
apricot	2354265.87	3922718.88	1568453.01	66.0455366
blueberry	3622185.36	2199023.04	-1423162.3	-40.24475
carob	1720935.76	3058316.89	1337381.13	76.9471877
cherry	4128295.36	4293391.76	165096.405	3.96469352
cranberry	546601.86	645084.389	98482.5294	46.2373844
gooseberry	4491385.19	4002593.34	-488791.85	-10.873489
grape	2153349.41	3704148.69	1550799.28	72.4024069
kiwi	2459537.65	3717285.48	1257747.83	58.638474
peachetc	2423274.19	3782216.87	1358942.68	55.7807432
pear	1084403.53	2129646.58	1045243.05	96.3052426
plum	3456835.95	4129752.97	672917.023	19.8894947
rasberry	3947170.44	4180453.07	233282.632	6.11115364
sourcherry	3760152.95	4141158.58	381005.63	10.1011873
strawberry	3020040.72	3727927.12	707886.396	24.8113889
tangetc	2641468.41	4805519.25	2164050.84	82.105503
fig	2098212.97	3598939.13	1500726.16	71.1844379
avocado	442700.232	924957.268	482257.035	108.592634
cashew	0	0	0	NA
citrusnes	0	0	0	NA
date	95848.7401	65524.5744	-30324.166	-32.3668
grapefruitetc	88096.5409	301692.139	213595.598	264.376279
groundnut	360223.515	1280887.14	920663.623	271.596388
karite	0	0	0	NA
lemonlime	301834.608	520810.362	218975.754	78.6876135
mango	0	0	0	NA
olive	861743.972	1748886.34	887142.363	102.755451
orange	200688.452	442227.607	241539.156	123.208597
papaya	49311.7466	0	-49311.747	-100
persimmon	1987636.22	3501629.54	1513993.33	76.0373234
pineapple	430.807814	921.490115	490.682301	NA
pistachio	456365.956	1291113.07	834747.119	187.788686
plantain	5615103.38	5615336.41	233.03306	0.00415061
quince	2440740.84	3640325.98	1199585.14	48.9565925
areca	1225608.59	1146203.51	-79405.076	12221.1478
barley	5483908.27	5319558.95	-164349.31	-2.9930095
bean	3986138.84	5019217.21	1033078.38	26.162475
broadbean	4523421.53	5459579.41	936157.883	22.4770532
buckwheat	4132220.52	4985504.77	853284.251	20.8368679
castor	17.2217734	0	-17.221773	NA
chickpea	359196.18	246317.458	-112878.72	NA
cowpea	0	0	0	NA
maize	5016768.07	5361862.26	345094.182	6.88229005
oats	5484365.6	4980559.93	-503805.67	-9.1800933
pea	5340716.25	5208528.7	-132187.54	-2.4687154
pigeonpea	0	146.126991	146.126991	NA

rapeseed	3368748.57	3896716.35	527967.778	16.4127488
rice	578870.708	1389540.6	810669.897	141.057513
rye	3760677.78	2711360.28	-1049317.5	-28.097845
sorghum	479847.972	1601665.7	1121817.73	230.581283
soybean	1344377.17	2657540.3	1313163.12	100.645407
triticale	4333674.81	3094276.15	-1239398.7	-28.494682
wheat	5341128.65	5546053.11	204924.457	3.84789031
greenbean	3349525.25	4216034.02	866508.773	26.3584221
greencorn	3272023.3	4076237.15	804213.847	25.4116333
greenpea	3095990.66	4423240.78	1327250.12	44.3873504
alfalfa	3839838.41	5233728.09	1393889.68	37.9436615
beetfor	1896115.79	1312058.07	-584057.72	-30.667721
cabbage	1491567.19	2731042.87	1239475.68	83.0245331
carrot	4516350.95	5061983.94	545632.99	12.0553394
cassava	3853.84541	29.7554671	-3824.0899	-99.336511
cauliflower	478410.545	1203873.79	725463.248	151.451298
chilleetc	2190062.04	3255059.26	1064997.22	48.6295682
clover	2728040.96	2160340.95	-567700.01	-20.834906
cucumberetc	1943609.88	3224528.21	1280918.32	64.4833253
eggplant	1017945.04	1911807.82	893862.774	88.3361704
grassnes	3031526.96	3511872.56	480345.599	16.464193
lettuce	1261279.08	1607526.58	346247.508	26.6766838
melonetc	2118733.94	3208257.38	1089523.44	50.3885228
okra	0	233.010643	233.010643	NA
onion	2977529.51	3695368.81	717839.306	24.3864615
potato	5349118.52	5398754.72	49636.2036	0.96707098
pumpkinetc	2109917.57	2775523.21	665605.634	31.1538486
spinach	1492262.62	2583424.14	1091161.52	73.1150613
swedefor	604391.042	119701.621	-484689.42	-79.639466
sweetpotato	1493585.46	3516516.26	2022930.8	135.217303
taro	1527.14398	9465.86866	7938.72468	298.653776
tomato	2870242.17	3644148.53	773906.361	26.7002892
turnipfor	490470.504	296650.766	-193819.74	-37.884101
watermelon	1330132.79	2743961.14	1413828.35	105.755389
cinnamon	0	405.547184	405.547184	NA
cocoa	0	0	0	NA
coconut	0	0	0	NA
coffee	50060.1774	95797.9368	45737.7594	104.511194
cotton	305475.106	1417421.39	1111946.28	364.758762
flax	5204417.01	5512945.49	308528.482	5.93108332
hemp	2721088.4	3967131.57	1246043.17	46.5180414
kapokseed	189.093776	0	-189.09378	NA
oilpalm	0	0	0	NA
pimento	92344.6063	289946.602	197601.996	385.122641
ramie	1477414.75	4100123.22	2622708.47	181.05325
rubber	0	0	0	NA
sugarcane	28340.9642	176610.8	148269.835	1139.11216
sunflower	3568303.75	4547492.76	979189.007	27.9383825
tobacco	2541010.4	3610495.4	1069484.99	41.5006953
Abies alba	1492479.69	919435.226	-573044.47	-37.607238
Acer campestre	6953244.25	7541805.13	588560.878	8.48154223

Acer platanoides	5608296.41	5798058.95	189762.534	3.38642812
Acer pseudoplatanus	3868408.35	4018327.01	149918.658	4.10225379
Alnus glutinosa	5198083.05	5829599.8	631516.745	12.2188155
Betula pendula	5286766.76	4540247.06	-746519.69	-14.11471
Castanea sativa	3309709.78	4645142.75	1335432.97	40.2826023
Corylus avellana	4614749.69	5046613.31	431863.622	9.40347802
Eucalyptus globulus	625881.757	1194147.72	568265.963	91.10437
Fagus sylvatica	4013382.14	4347870.75	334488.605	8.3182686
Fraxinus excelsior	6104329.79	6634397.86	530068.073	8.72316745
Juglans regia	4980098.15	5888650.23	908552.073	18.8525898
Larix decidua	902888.649	400496.99	-502391.66	-54.984924
Picea abies	3326374.67	2014187.22	-1312187.4	-39.468556
Pinus nigra	3772055.49	5094948.59	1322893.1	35.5377123
Pinus pinaster	1921573.24	2990659.69	1069086.45	55.6045355
Pinus pinea	647679.921	1318965.37	671285.448	101.480365
Pinus sylvestris	4595767.54	3172867.33	-1422900.2	-31.024946
Populus alba	4365130.89	5828611	1463480.11	33.5333944
Populus nigra	6894700.78	7646445.37	751744.585	10.9343351
Populus tremula	6988862.72	6304708.9	-684153.82	-9.7952038
Prunus avium	5412977.54	6206020.49	793042.958	14.6701209
Pseudotsuga menziesii	3986621.83	4225875.59	239253.762	6.05085763
Quercus petraea	4994663.78	5828703.96	834040.175	16.7908093
Quercus robur	5892440.7	6235103.27	342662.572	5.84095851
Quercus suber	1057426.45	2020201.65	962775.196	90.7019568
Robinia pseudoacacia	3739009.05	4504309.99	765300.937	21.1411671
Salix alba	4347579.68	5033856.72	686277.04	15.8552175
Tilia cordata	6234680.16	6160419.61	-74260.545	-1.1992308
Ulmus laevis	5892354.77	5636339.97	-256014.8	-4.3236439

Supplementary Table 7: Pest species, description of their native and invasive and the geographical origin of their occurrence records.

Species name	Native range	Invasive range	Records
Acleris variana	North America		Full
Agrilus anxius	North Amercia	Southern Africa	Full
Agrilus planipennis	East Asia	North America	Full
Aleurocanthus spiniferus	South Asia	Africa, Australia	No records in Africa and Australia
Aleurocanthus woglumi	South Asia	Africa, North America, Central America, South America, Oceania	Only 2 records from native range
Anastrepha fraterculus	South America, Central America		Full
Anastrepha ludens	Central America		Full
Anastrepha obliqua	South America, Central America		Full
Anoplophora glabripennis	China	North America	Only 3 records in North America, 2 records in Europe
Anthonomus bisignifer	Japan	Russia	Native range only
Anthonomus grandis	Central America	North America, South America	Full
Anthonomus quadrigibbus	North America		Full
Anthonomus signatus	North America		Full
Bactericera cockerelli	North America	Central America; New Zealand	Full
Bactrocera cucumis	Australia		Full
Bactrocera cucurbitae	South Asia	Africa	Full
Bactrocera invadens	Sri lanka	Africa	Full
Bactrocera latifrons	Asia	Africa, Hawaii	Full
Bactrocera tryoni	Austalia		Full
Bactrocera zonata	Asia	West Asia, Africa	Full
Ceratitis rosa	East and South Africa		Full
Choristoneura conflictana	North America		Full
Choristoneura freemani	North America		Full
Choristoneura rosaceana	North America		Full
Conotrachelus nenuphar	North America		Full
Dacus ciliatus	Africa, Asia		Full
Dendroctonus adjunctus	North America		Full
Dendroctonus brevicomis	North America		Full
Dendroctonus frontalis	North America, Central America		Full
Dendroctonus ponderosae	North America		Full
Dendroctonus pseudotsugae	North America		Full
Dendroctonus rufipennis	North America		Full
Dendrolimus superans	Japan, Russia		Only 4 records in Russia
Diabrotica barberi	North America		Full
Diabrotica speciosa	South America		Full
Diabrotica undecimpunctata howardi	North America		Full
Diabrotica undecimpunctata undecimpunctata	North America		Full

Diaphorina citri	South Asia	South America, Central America, North America, East Africa	No records from Africa
Epitrix cucumeris	North America	Central America	Full
Epitrix subcrinita	North America	South America	Native range only
Euwallacea fornicatus	Asia	North America, Central America, Oceania	No records from Central America
Gnathotrichus sulcatus	North America	Central America	Full
Gonipterus scutellatus	Australia	South America, Africa, Southern Europe	No records from South America
Grapholita packardi	North America		Full
Helicoverpa zea	North America, Central America, South America		Only 1 record in South America
Heteronychus arator	Africa, Oceania		Full
Homalodisca vitripennis	North America		Full
Ips calligraphus	North America, Central America	Philippines	Native range only
Ips grandicollis	North America, Central America	Oceania	Only 3 records in Oceania
Ips pini	North America		Full
Leucinodes orbonalis	Asia, Oceania		Only 3 records in Oceania
Limonius californicus	North America		Full
Liriomyza sativae	China	Africa, North America, Central America, South America, Oceania	Invasive range only
Listronotus bonariensis	South America	Oceania	Full
Lycorma delicatula	Asia	North America	Only 4 records in North America
Lymantria mathura	Russia, East Asia		Full
Maconellicoccus hirsutus	Southern Asia	Africa, Oceania, North America, Central America, South America	No records in Asia and only 1 record in Africa
Malacosoma americanum	North America		Full
Malacosoma disstria	North America		Full
Massicus raddei	China, Japan	Russia	Only two records not from Japan
Megacopta cribraria	Asia	North America	Invasive range only
Melanotus communis	North America	Melanotus communis	Full
Metamasius hemipterus	Central America, South America	Africa	Native range only
Naupactus leucoloma	South America	North America, Australia, South Africa	Only 1 records from Africa
Naupactus xanthographus	South America		Full
Neodiprion abietis	North America		Full
Oemona hirta	New Zealand		Full
Orgyia pseudotsugata	North America		Full
Pissodes strobi	North America		Full
Platynota stultana	North America		Full
Polygraphus proximus	Russia, East Asia		Full
Popilia japonica	Japan	North America, Russia, Southern Europe	No records in Russia
Pseudacysta perseae	North America, Central America, South America	Portugal	No records in Soth America

Rhagoletis mendax	North America		Full
Rhagoletis pomonella	Western USA	Eastern USA	Full
Rhynchophorus palmarum	Central America, South America		Full
Saperda candida	North America	German Island	Full
Scirtothrips dorsalis	South Asia, Oceania	South Africa, Hawaii, Carribean, Israel	No records from South Africa and Hawaii
Spodoptera eridania	South America	North America, Central America	Only 4 records in South America
Spodoptera frugiperda	South America	Africa, Asia	No records in Asia
Spodoptera litura	South Asia	East Asia, Oceania	Full
Strauzia longipennis	North America	Germany (1 record)	Full
Tecia solanivora	Central America, South America	Tenerifa	Full
Thaumatotibia leucotreta	Africa		Full
Trioza erytreae	Africa	Saudi-Arabia, Portugal	Full
Xylosandrus compactus	Asia	Africa, North America, Central America, South America, Oceania	Invasive range only
Xylosandrus crassiusculus	Asia	Africa, North America, Central America, Oceania	No records in Oceania and little records in Asia and Africa
Zaprionus indianus	Africa	Asia, North America, Central America, South America, Southern Europe	No records in Europe
Zaprionus tuberculatus	Africa	Mediterranean	Only 1 record in Italy

CHAPTER II

Inflection point in climatic suitability of insect pest species in Europe suggests non-linear responses to climate change

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Abstract

Climate change and globalization affect the suitable conditions for agricultural crops and insect pests, threatening future food security. It remains unknown whether shifts in species' climatic suitability will be linear or rather non-linear, with crop exposure to pests suddenly increasing when a critical temperature threshold is crossed. Moreover, uncertainty of forecasts can arise because of the modelling approach based either on species distribution data or on physiological measurements. Here, we compared the predictions of two modelling approaches (physiological models and species distribution models) for forecasting the potential distribution of agricultural insect pests in Europe. Despite conceptual differences, we found good agreement overall between the two approaches. We further identified a potential regime change in pest pressure along a temperature gradient. With both modelling approaches, we found an inflection point in the number of pest species with suitable climatic conditions around a minimum temperature of the coldest month of -3°C. Our results could help decision-makers anticipate the onset of rising pest pressure and provide support for intensifying surveillance measures, particularly in regions where temperatures are already beyond the inflection point.

Keywords: agricultural crop, climate change, insect pest, physiological model, species distribution model, temperature threshold

Introduction

Climate change is predicted to shift the distribution of agricultural crops and of the insect pest species feeding on them (Tubiello et al., 2007; Bebber, Holmes & Gurr, 2014; Sloat et al., 2020). While changing climatic conditions might increase climatic stress factors and reduce resources for water irrigation of crops (Fader et al., 2016), higher temperatures favour the expansion of cultivation and crop diversification at higher latitudes (Tuck et al., 2006; Walther et al., 2002; Grünig et al., 2020). However, climate change is also associated with greater pest pressure (Deutsch et al., 2018). Further, trade flows and human travel help insect pests to overcome natural barriers, linking climate change and globalization to pest invasions (Robinet & Roques, 2010; Hulme, 2009; Paini et al., 2016). Distribution ranges of pest species are expected to shift, to the detriment of cropping systems (Bebber et al., 2013), and thus threaten food production (Schmidhuber & Tubiello, 2007) and undermine increasing consumer demands for local and more sustainably produced food (Lamichhane et al., 2016; Feldmann & Hamm, 2015). Investigating the distribution of niches of pest species along climatic gradients can point to future opportunities and risks under climate change (Grünig et al., 2020) and help develop effective crop-protection strategies.

The development of insects is a function of temperature over time (Jarosik et al., 2011). Under climate change, temperatures in Europe, particularly at higher latitudes, are expected to increase more than the global average warming (MacDonald, 2010; IPCC, 2007). Ongoing warming allows the cultivation of more crops (Maracchi, Sirotenko, & Bindi, 2005) but also favours insect pest survival in these regions (Bale & Hayward, 2010). Higher winter temperatures are crucial for the survival of insect pest species at higher latitudes (Bebber et al., 2013; Jarosik et al., 2015), although in practice their realized distribution is restricted by additional factors, particularly biotic interactions (Hutchinson, 1957). To account for the multitude of factors that potentially define the climate suitability for insect pests, different modelling approaches have been developed, which should imply differences in predictions (Roberston et al., 2003; Kearny, Wintle & Porter, 2010; Newman, 2005).

To model the climatic niche of pest species, deductive and inductive approaches have been developed (Venette et al., 2010; Tonnang et al., 2017). For the deductive approach adopted in physiological models, data from controlled experiments provide a basis to project the potential distribution of a species (Tonnang et al., 2017). Studies on the life history of species under different environmental conditions help define physiological thresholds for species survival, development and performance, which are often used to develop phenological models (e.g. Schaub et al., 2017). By relating these thresholds to climatic variables in a spatial context (e.g. spatial raster layers of temperature), areas where species meet conditions that allow their development can be identified (Kearney & Porter, 2004; Kearney & Porter, 2009). Inductive models use the occurrence records of a species and link them to climatic data to infer the conditions that are suitable for the species (Guisan & Zimmermann, 2000; Elith & Leathwick, 2009). Species distribution models (SDMs) implementing the inductive approach have been widely used to model climatic suitability of insect pests (e.g. Arthur, Morrison & Morey, 2019). While deductive and inductive modelling approaches target similar goals of mapping suitable climatic conditions for a species in space, they differ in terms of the data used for model development. A better understanding of how systems can be expected to shift under climate change could potentially be achieved by comparing forecasts between those approaches.

The response of a biological system to climate change can be linear or non-linear. When the response is not linear, the ecosystem state typically shifts faster than what would be expected for a linear response (Dakos et al., 2019), eventually exhibiting discontinuities when critical thresholds in the driving variables are crossed (Lenton, 2011). Shifts in pest distributions under climate change may display discontinuous behaviour, implying a sudden change in the potential for colonization by pest species, including the invasion of non-native species, as a result of global warming (Paini et al., 2016). Invasive insects are likely to be introduced from geographic areas sharing similar climatic conditions (Brockerhoff & Liebhold, 2017; Walther et al., 2009). With climate change, temperate regions will become warmer and therefore climatically more similar to regions where insect diversity is presently disproportionally higher. The study of pest species' climatic niches coupled with climate change scenarios help identify potential inflection points for pest suitability.

Here, we investigated the potential pest accumulation in Europe under climate change by comparing predictions obtained from deductive physiological models and inductive SDMs. We considered a comprehensive set of insect pests that includes a large number of quarantine insects. We evaluated whether climatic niches shift along a smooth gradient, or whether an inflection point exists, beyond which the increase in the number of potential niches accelerates. Our working hypotheses were as follows:

i) We expected congruent forecasts of suitable climate with the two modelling approaches. Under climate change, we expected a general pattern of increasing climatic suitability for insect pests across Europe, irrespective of the modelling approach applied.

ii) We expected non-linear responses to minimum temperatures for insect pests, involving thresholds beyond which the number of species with a suitable climate increases considerably.

iii) We expected to observe that temperatures in Southern Europe already exceed the threshold temperature identified under (ii). Hence, we expected to find that these regions already provide suitable climatic conditions for many insect pest species because temperatures rarely dip below freezing.

Materials and Methods

Physiological data collection

For physiological data, we assembled insect developmental thresholds from the PRATIQUE database (Jarosik et al., 2011) and published literature. From the PRATIQUE database, we selected insect species classified as pests in the EPPO Global Database (www.eppo.org), which comprises information generated or assembled by the European and Mediterranean Plant Protection Organization. Further, we searched on GoogleScholar for studies applying CLIMEX models for pest species (keyword combinations of "*CLIMEX*" + "*insect*" + "*pest*"). We obtained physiological parameters on the lower development threshold (LDT; minimum development threshold in CLIMEX studies) and the sum of effective temperatures (SET), that is, the number of growing degree days above the LDT required for the completion of a generation. LDTs and SETs reflect a linear relationship between developmental rate and temperature, and are calculated from the proportion of development occurring per unit of time (Jarosik et al., 2011). Where multiple entries per species were available, we used the average of the values. Further, we searched for lethal temperatures of all species. Whenever we did not find a lower lethal temperature ($\boldsymbol{T_{kill,min}}$), we set it to 0°C for species not known to survive winter in a dormant stage and to -20°C for species with winter diapause. This implies that warm-adapted species are predicted to not occur in regions where the minimum temperature of the coldest month is below 0°C. We used 40°C as the upper lethal temperature

($\boldsymbol{T_{kill,max}}$) for all species, as insects are known to have little variability in this regard, with values ranging from 40°C to 50°C (Heinrich, 1981). We collected data on physiological parameters for 75 species (Table S1 in the Supplementary Material).

Occurrence data collection

We compiled the distribution records of pest species in the published literature and the Global Biodiversity Information Facility (GBIF, www.gbif.org) for all pest species in the EPPO Global Database. We searched Google Scholar for the following keywords in various combinations: "*Pest name*", "*distribution*", "*records*", "*occurrence*", "*sampling*", "*spatial*" and "*data*". GBIF data were carefully checked for unreliable records. We classified the pest species into two categories: all species on the EPPO quarantine lists (A1, A2, Alert) were considered quarantine pests, and all others established pests. Species for which we could not obtain more than 20 occurrence records were dismissed (Wisz et al., 2008). In total, we gathered occurrence data for 173 species (Table S2).

Climate data and future scenarios

We acquired climate data from the CHELSA database (www.chelsa-climate.org). We used CHELSA V1.2 data for monthly minimum, maximum and mean temperatures, as well as bioclimatic variables, with a 2.5 arcmin (5 km) grid size resolution (Karger et al., 2017) to represent current climatic conditions. Further, we used climate change scenarios from the CMIP5 family representing two different scenarios (RCP 4.5, RCP 8.5) and four global circulation models (GCMs). We selected the following GCMs based on model interdependence to achieve a good representation of uncertainty in climate projections (Sanderson et al., 2015): CESM1-BGC (US National Center for Atmospheric Research, NCAR); CMCC-CM (Centro Euro-Mediterraneo per i Cambiamenti Climatici, CMCC); MIROC5 (University of Tokyo); and ACCESS1-3 (Commonwealth Scientific and Industrial Research Organization, CSIRO, and Bureau of Meteorology, BOM, Australia).

Physiological models

We developed physiological models by coupling physiological data with monthly mean, minimum and maximum temperatures following FAO-ECOCROP (Hijmans et al., 2001; Ramirez-Villegas et al., 2013) and CLIMEX (Sutherst & Maywald, 1985) approaches. The output of the models is a suitability index (Si) calculated on cell basis of a spatial raster (5 km). As a global equation, we calculated Si as the product of a temperature index (Ti), a growing index (Gi) and a killing index (Ki) (equation 1).

$$\boldsymbol{Si = Ti * Gi * Ki} \tag{1}$$

Ti was calculated as the fraction of months in which the monthly mean temperature (T_k) exceeds LDT (equation 2).

$$\boldsymbol{Ti = \frac{1}{12}\sum_{k=1}^{12} p_k} \tag{2}$$

with

$$\boldsymbol{p_k = \begin{cases} 1 & if\ \overline{T}_k > LDT \\ 0 & otherwise \end{cases}}$$

We evaluated Gi based on the growing degree days needed for completion of development (GDD_{req}) (equation 3).

$$\boldsymbol{Gi = \begin{cases} 0 & if\ \sum_{k=1}^{12}(\overline{T}_k - LDT) < GDD_{req} \\ 1 & otherwise \end{cases}} \tag{3}$$

For Ki, we checked whether the monthly minimum temperature ($T_{min,k}$) fell below the lethal minimum temperature ($T_{kill,min}$) and whether the monthly maximum temperature ($T_{max,k}$) surpassed the lethal maximum temperature ($T_{kill,max}$) (equation 4).

$$\boldsymbol{Ki = \prod_{k=1}^{12} m_k \prod_{k=1}^{12} n_k} \tag{4}$$

with

$$\boldsymbol{m_k} = \begin{cases} \mathbf{1} & \boldsymbol{if\ \overline{T}_{min,k} > T_{kill,min}} \\ \mathbf{0} & \boldsymbol{otherwise} \end{cases}$$

$$\boldsymbol{n_k} = \begin{cases} \mathbf{1} & \boldsymbol{if\ \overline{T}_{max,k} < T_{kill,max}} \\ \mathbf{0} & \boldsymbol{otherwise} \end{cases}$$

We evaluated the physiological models using a maximum sensitivity approach based on occurrence data. To calculate the sensitivity of the model predictions, we projected the models to a global extent in order to include all available occurrence records for the evaluations. Models with a sensitivity score < 0.5 were excluded from the analyses. The outputs were classified into binary predictions using the maximum sensitivity threshold calculated with the *optimal.thresholds* function in the 'PresenceAbsence' package (version 1.1.9; Freeman & Moisen, 2008).

Species distribution models

SDMs were calibrated using ensembles (unweighted averages) of generalized linear models (GLMs) and generalized additive models (GAMs; Wood, 2006). For each species, we randomly sampled 5,000 pseudo-absences from the species biomes. We weighted presence records in order to balance their weights with the large number of pseudo-absence records. We assumed a binomial error distribution for both modelling techniques and used fourth-order polynomials to adjust the flexibility of the response curve. As predictor variables, we used growing degree days above 5°C and minimum temperature of the coldest month to reflect the variables used in the physiological models. We used a variable selection procedure to reach an acceptable model performance and projection for as many species as possible (see Note S1). Further, we followed the standards and guidelines for distribution modelling (Araujo et al., 2019). GLMs were fitted with the 'base' R-package, whereas GAMs were fitted with functions in the R-package 'gam' (version 1.16.1; Hastie, 2019). For the evaluation of model performance, we used a split sample approach (70% calibration data and 30% evaluation data) with 20 repetitions to calculate the area under the ROC-plot curve (AUC) and true skill statistics (TSS). We considered models to be reliable at AUC > 0.7 (Hosmer, Lemeshow & Sturdivant, 2013) and TSS > 0.4 (Descombes et al., 2015) and discarded all others. Additionally, we inspected the quality of all model projections visually. For binary classifications of the model outputs, we used the optimal TSS threshold (Allouche et al., 2006).

Comparison of physiological and species distribution models

For each species with reliable projections in both modelling approaches, we calculated the Pearson correlation coefficient between the predicted suitability indices of the two model projections and the percentage of agreeing grid cells of the binary projections. Further, we calculated the Sørensen index for the community similarity between the modelling approaches. For this, we stacked together the predicted binary projections of all species for each timestep, resulting in species richness raster stacks for the different modelling approaches for each timestep. For these raster stacks we calculated the Sorensen dissimilarity index with the *beta.pair* function of the 'betapart' R-package (version 1.5.1; Baselga et al., 2018), which we then subtracted from 1 to obtain a similarity index ranging from 0 to 1, where 1 indicates complete agreement for the exact same set of species and 0 no overlap between the predicted communities. To quantify differences between projections of the two modelling approaches (i.e. absolute model agreement), we subtracted the model projection of the SDM from the physiological model projection for each species and summed the resulting differences across all species. Positive values indicate overrepresentation by the physiological models, and negative values signify overrepresentation by the SDMs.

Analysis of inflection points under climate change

Based on the predicted distribution in Europe for each species under current climatic conditions, we calculated the relationship between the predicted occurrence and the minimum temperature of the coldest month by extracting values from all grid cells in the study area. Minimum temperature represents the most limiting factor for insect distributions (Jarosik et al., 2015). We calculated the average probability of occurrence for each temperature class (step of 0.1°C). We identified the turning-point temperature, marking the border of the climatic niche, for each species by fitting GAMs, using the R-package 'mgcv' (version 1.8-31; Wood, 2011), for the relationship between minimum temperature of the coldest month and average probability for the temperature class. For this, we extracted minimum temperatures, corresponding to occurrence probabilities in the range 0.4 to 0.6 (in steps of 0.05) from the fitted values of the GAM (Figure S1). We ordered species according to the turning-point temperature and then investigated the shape of the pattern of the number of species along the temperature gradient.

We used the 'segmented' R-package (version 1.1.0; Muggeo 2003) to identify breakpoints, which mark a change in slope in the ordered sequence of turning-point temperatures. To find a suitable initial estimate of the number and location of the breakpoints, we used the final estimates of the breakpoints and the slopes of the linear regression models for the intervals between the breakpoints. We isolated the slopes of the two distinct clusters of niches and scaled them to the relative number of species used for each modelling approach. Finally, we mapped the breakpoint temperatures marking the end of the first cluster, the start of the second cluster and the end of the second cluster to highlight the areas that are likely to become climatically suitable for warm-adapted pests and potentially see a rapid accumulation of newly occurring pests. We used representative values of -6°C, 0°C and 6°C as limits for these domains, taking into account the good agreement between the breakpoints identified for the two different modelling approaches (Figure S2).

To determine the inflection point marking the transition between the first and the second cluster of pest species, we fitted a GAM to the ordered turning-points for each cut-off threshold (0.4–0.6) and identified the inflection point temperature with the function *ese* in the 'inflection' R-package (version 1.3.5; Christopoulos, 2016). We compared the AIC values of the GAMs with linear functions to check whether the data follows a non-linear distribution (Table S3). We calculated the mean and the confidence interval (0.95%) for the inflection zone from the inflection points of the different cut-off thresholds. All analyses were done in R version 3.6.3 (R Core Team, 2020).

Results

Model performance and niche limits

The development thresholds varied widely over the study species (Figure S3). LDTs were between 1.6°C and 15°C. Degree days required to complete development ranged from 148 to 1800 and minimum killing temperature ranged from -40°C to 4.5°C. We obtained acceptable model sensitivity (> 0.5) for all 75 species, with a median of 0.97. We found lower niche limits between -19.3°C and 10.8°C, with a median over all species of -7.7°C. The upper niche limit was the same for all species (12.4°C) and the median niche breadth was 20.3°C. For SDMs, we gathered occurrence records for 173 pest species. We obtained satisfying model performance for 159 pest species, with a median model performance of 0.83 in terms of AUC score and 0.59 for TSS. We found lower niche limits between -22.8°C and 11.9°C, and upper limits between -4.4°C and 12.4°C. The median lower niche limit was 0.1, whereas the median upper niche limit was 12.4°C. We estimated a median niche breadth of 9.2°C.

Agreement between modelling approaches

Generally, we observed good agreement between the two modelling approaches regarding pest species distributions, despite large variation among species and regions. Comparing the pair of model projections for all species, we found a median Pearson correlation coefficient between the occurrence probability predictions of the two modelling approaches of 0.68 under current climatic conditions, ranging from -0.8 to 0.88 and with a standard deviation of 0.31. For binary projections, this corresponded to agreement of predictions in 85% of the grid cells. For future climate change scenarios, the pairwise model agreement decreased until 2100, where we found a median Pearson correlation of 0.46 with higher uncertainty (standard deviation 0.48), corresponding to agreement in 70% of the grid cells (Figures S4 & S5). Concerning the spatial model agreement, we observed differences in the community similarity predicted by the two modelling approaches. Disagreement arose mainly in Northern and Northeastern Europe, as well as in mountain ranges (Figure 1). Under future projections, the community similarity increased towards Northeastern Europe, but decreased in southern regions. The cumulated model disagreement showed that SDMs were responsible for the discrepancies in southern regions, because they were more restricted at southern range borders (Figures S6 & S7). When comparing the niche breadth predicted by the two modelling approaches, we observed much broader niches predicted by physiological models than by SDMs. The median of the pairwise niche breadth difference was 3.8°C.

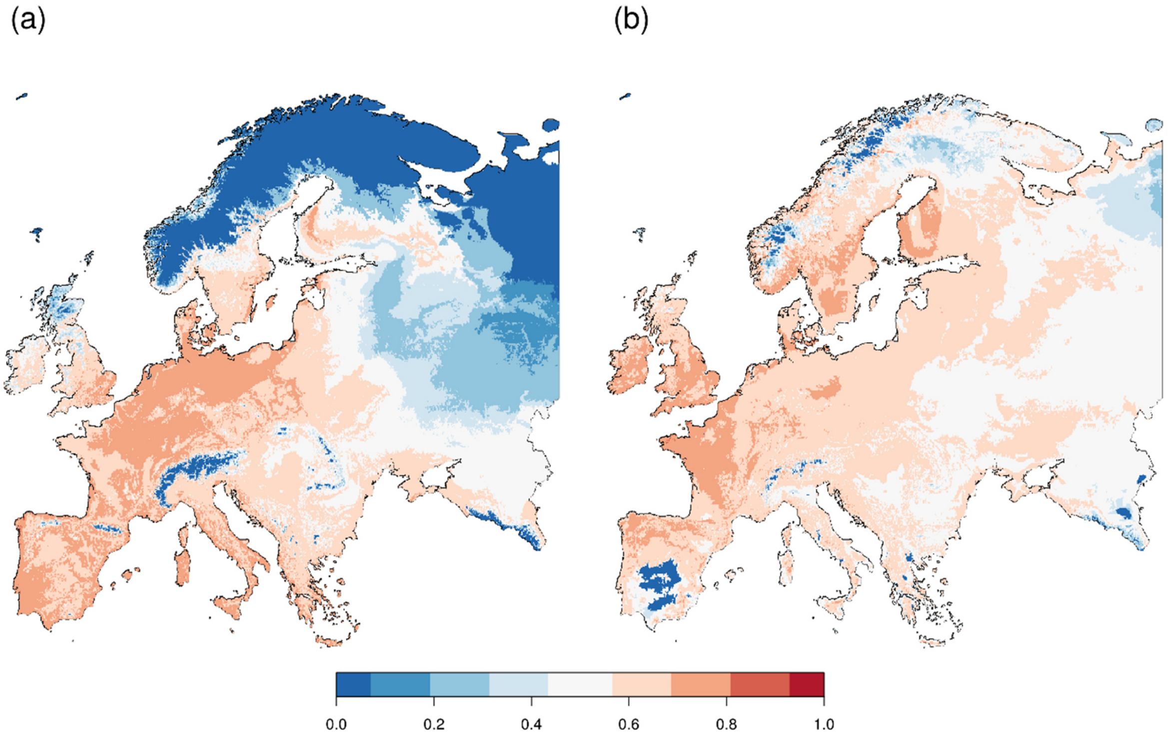

Figure 1: Maps of model agreement (Sørensen similarity index) for 2010 (a) and 2100 (b). Blue/red colours indicate lower/higher community similarity of predicted species. Results in (b) are based on the RCP8.5 climate change scenario (for results based on the RCP4.5 scenario, see Figure S8).

Shift in modelled pest distribution

Regarding changes in pest species richness over time, agreement between the modelling approaches was good over Central Europe and the UK (Figure 2), while in marginal areas (Eastern Europe, in particular Belarus and the Ukraine) changes were predicted differently by the two modelling approaches. We observed an increase in Northeastern Europe and mountainous regions of up to 30 species with physiological model projections and up to around 70 species with SDM projections. This corresponds to about 50% of species for physiological models and 40% for SDMs. When comparing the results of the different RCP scenarios, we found a greater increase in the number of species with a suitable climate under RCP8.5 than under RCP4.5. In particular, physiological models showed a much greater increase in northern regions by 2100. For SDMs, the increase across Europe was very similar under the two scenarios, but differences arose in southern regions (e.g. Iberian peninsula), where fewer species with suitable climatic conditions were predicted for the year 2100 under RCP8.5.

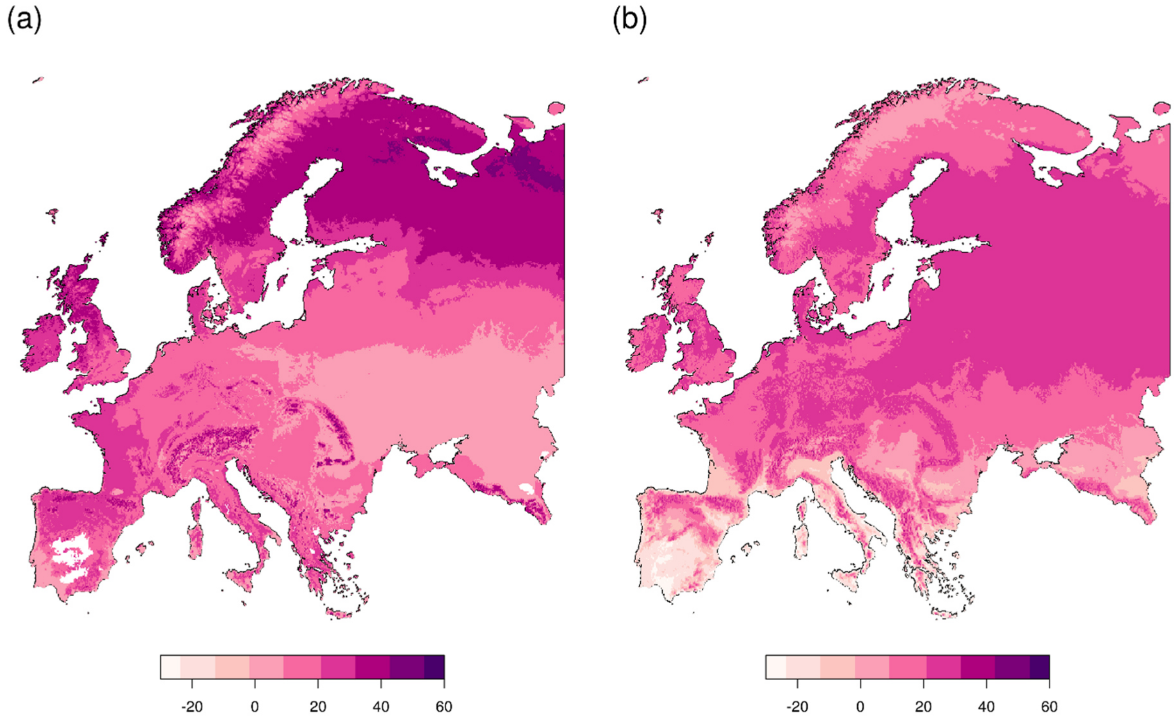

Figure 2: Change in the number of species between 2010 and 2100, as predicted by (a) physiological models and (b) SDMs. The number of modelled pest species was higher for the SDMs (159) than for the physiological models (75), and we therefore scaled the changes to 100 species to enable model comparison despite this difference. The white area in central Spain marks the region where maximum monthly temperatures above the assumed upper lethal temperature of 40°C in 2100 prevented species occurrence. Results shown here are based on the RCP8.5 climate change scenario (for results based on the RCP4.5 scenario, see Figure S9).

Relationship between predicted niche distribution and temperature

We observed a non-linear relationship between species richness and temperature with the physiological models and SDMs (Figure 3). Temperature niches showed two distinct groups with both modelling approaches. The first group included cold-adapted species, predicted to occur in regions that experience minimum temperatures of the coldest month below the breakpoint temperature of -6°C. The second group consisted of warm-adapted species, existing only in regions where minimum temperatures of the coldest month never fall below the breakpoint temperature of 0°C. For both modelling approaches, there was only a partial overlap between cold-adapted and established species, and between warm-adapted and quarantine pests. In the warm-adapted group, quarantine species were overrepresented (Figure S10). The inflection point, marking the switch between the two groups, i.e. the inflection point, corresponded to a minimum temperature of the coldest month of -3.0°C for physiological model predictions and -3.1°C for SDM predictions. Additionally, we calculated inflection points for the subset of species for which we generated physiological models and SDMs (53 species). Including only these species, we observed inflection points at -3.0°C (physiological models; ±1.5°C) and -1.7°C (SDMs; ±1.5°C).

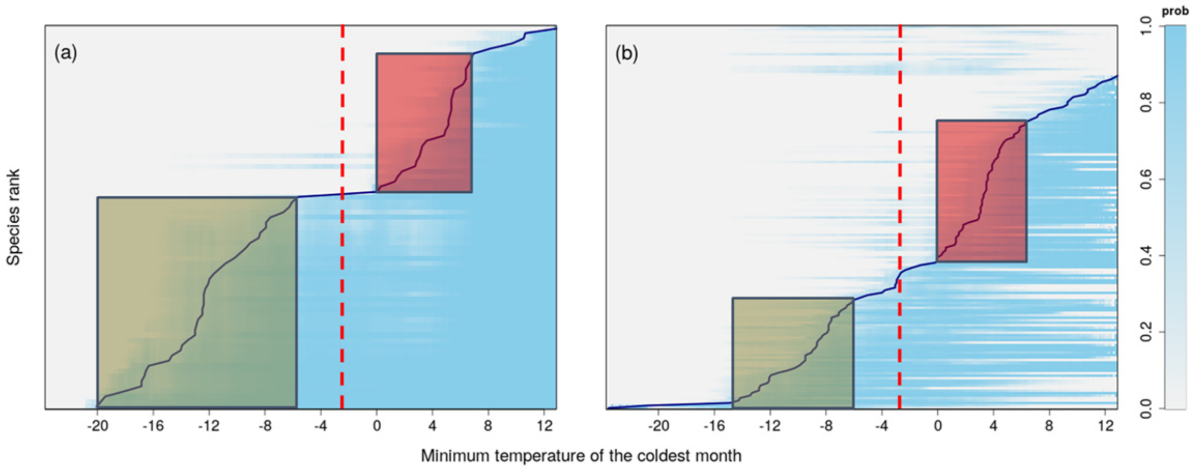

Figure 3: Climatic niches of pest species along a gradient of the minimum temperature of the coldest month. Light blue areas show the range in the climatic niche predicted by the physiological models (a) and SDMs (b) for each species, sorted by the turning-point temperature obtained with a cut-off threshold of 0.5. Denser blue for the temperature range of a species corresponds to a higher proportion of grid cells with this temperature predicted to be suitable for the species (prob). The dark blue lines show the distribution of turning-point temperatures. Inflection points were identified at -3.0°C for physiological model predictions and -3.1°C for SDMs (indicated by the red dashed lines). Yellow boxes indicate the group of cold-adapted species (up to the breaking point of -6°C) and red boxes the group of warm adapted species (between the breaking points of 0°C and 6°C). For the subset with 53 species, see Figure S11.

The spatial dynamics of the inflection point indicated clear shifts towards the northeast (Figure 4). The breakpoints (-6°C, 0°C, 6°C) are predicted to be dislocated at different rates. While the area above the -6°C isoline, marking the border of suitability for all cold-adapted species, almost covered the entire European continent, the other two isolines, marking the start and the end of the cluster of warm-adapted pests, were more stable. The area between 0°C and 6°C in Figure 4 corresponds to where warm-adapted species were predicted to encounter suitable climatic conditions. This area increased mainly in Western and Central Europe, but was predicted to reach the Atlantic coast of Norway in the North, as well as Poland and the coast of the Baltic Sea in the East, by 2100. Slopes of the increasing number of pests with suitable climatic conditions varied between the two groups. With physiological models we found an increase of about five species per degree for cold-adapted species and seven species per degree for warm-adapted species, and SDMs predicted four (cold-adapted) and seven (warm-adapted) species per degree.

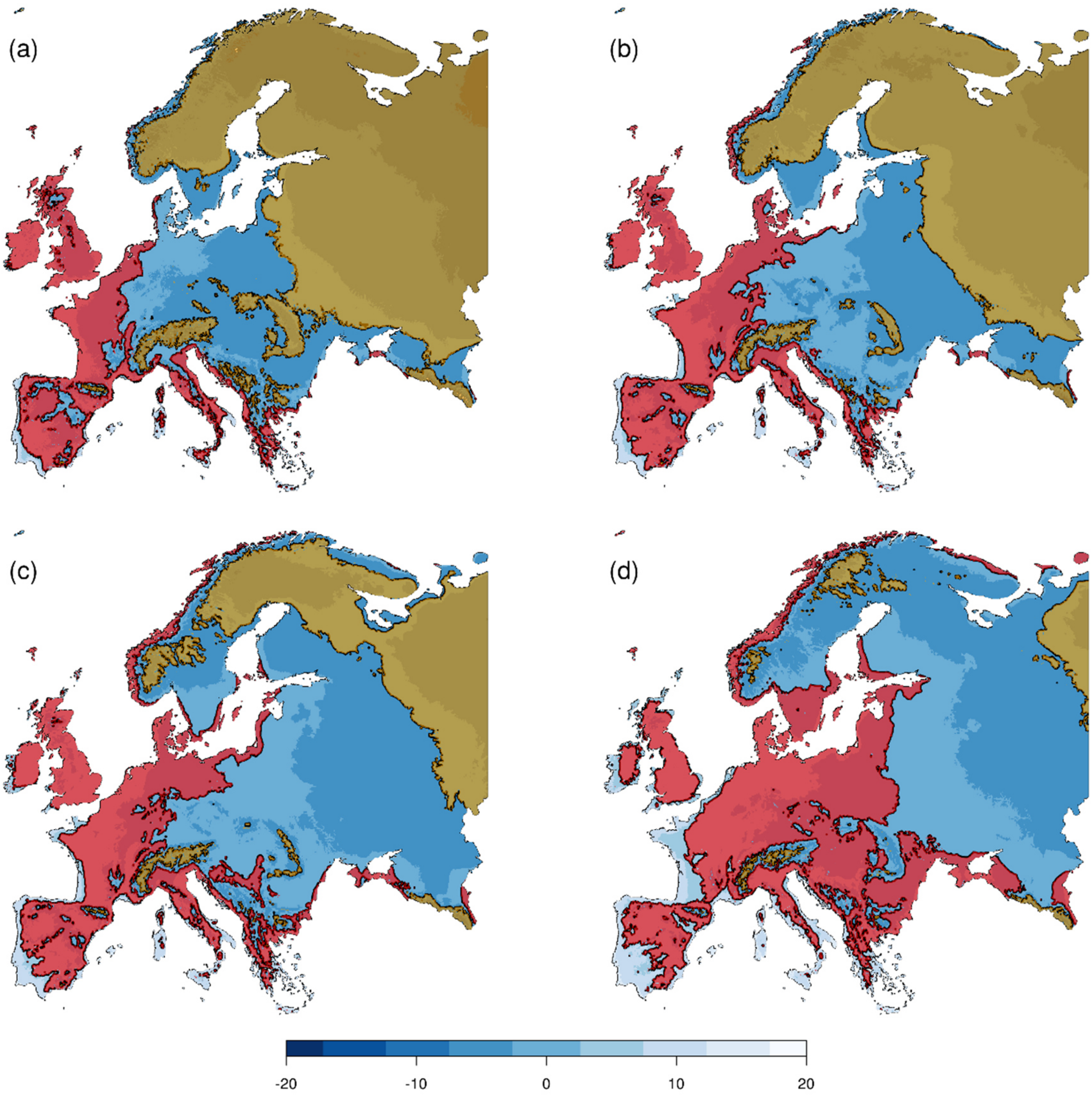

Figure 4: Figure 4: Spatial analysis of the inflection point across Europe. The maps show the minimum temperature of the coldest month across Europe in 2010 (a), 2040 (b), 2070 (c) and 2100 (d) under the RCP8.5 scenario. The yellow shaded area marks the region where minimum temperatures of the coldest month is below the -6°C breaking point. The red shaded area marks the region between the 0°C and the 6°C breaking points, where a strong acceleration of pest climatic suitability is expected. Figure S12 shows the results for the RCP4.5 scenario.

Discussion

In this study, we compared predictions of species distributions by physiological models and SDMs to investigate climatic niches of a comprehensive set of insect pest species of agricultural crops. Employing both physiological (deductive) and statistical (inductive) models entails robustness in cases of agreement and prompts interesting hypotheses when differences arise (Hijmans & Graham, 2006). We show general agreement in the predicted species distribution between the two modelling approaches. Moreover, with both modelling approaches, we found inflection points around -3°C in the minimum temperature of the coldest month, indicating increasing pest pressure after this threshold temperature is crossed.

Physiological and statistical models provide coherent results despite conceptual differences. Model projections for current climatic conditions showed good agreement for pairwise suitability index predictions 0.68), corresponding to 85% of the grid cells for binary projections. We found the highest model agreement in areas where both approaches predicted similar pest community composition to encounter suitable climatic conditions. We found lower similarity in Northern Europe (i.e. Scandinavia and the European part of Russia), as well as in high mountain ranges (Pyrenees, Alps and Carpathian Mountains), mainly because few insect pest species were predicted to occur in those regions. Furthermore, the niche breadth obtained from models reflects differences between the fundamental and the realized niche. We expected niches modelled based on physiological limits to be broader than realized niches (Venette et al., 2010; Soberón & Arroyo-Peña, 2017). The results confirmed this expectation, with realized pest niches predicted by SDMs (median niche breadth 9.2°C) much lower than fundamental climatic niches predicted by physiological models (17.1°C). Pairwise comparisons likewise suggested narrower climatic niches predicted with SDMs than with physiological models. The broader climatic niches predicted with physiological models indicates that SDMs may underestimate the climatically suitable area, implying that the regions of potential invasions could be larger than estimated based on SDMs alone. Yet, physiological models have also a methodological limitation regarding upper development thresholds, because data are not available for most species. Available data for 31 species indicated an average of 34.4°C, with only two species having their upper development thresholds below 30°C. Monthly mean temperatures above 34°C do not occur in Europe under the current climate and are unlikely to occur during this century (Figure S13) and thus it is unlikely that including upper development thresholds would have altered our predictions for pest species.

Forecasts of species distributions under climate change have been reported to be congruent for deductive and inductive models (Kearney, Wintle & Porter, 2010), although inductive models have also been reported to produce more pessimistic predictions than deductive models (Lobell & Asseng, 2017). Here, we found a decline in model agreement for future projections, with a decrease in median correlation from 0.68 in 2010 to 0.46 in 2100, although the latter value still represents relatively good agreement for binary projections (70%). We observed that the southern range borders modelled with physiological models remained mostly in the same locations, while SDM borders moved towards higher latitudes, resulting in lower community similarity in Southern Europe and decreasing model agreement. SDMs for future projections are more prone to extrapolation errors in areas where new climatic conditions will occur, which is not the case for physiological models (Kearney & Porter, 2009). This problem is particularly important for invasive species because the distribution is often projected to new environmental conditions (Elith, 2017), which could explain the decreasing model agreement and increasing differences in pairwise comparisons as time progresses.

On the individual species level, we observed differences between modelling approaches in the predictions of the area with suitable climatic conditions for a few species (e.g. *Dendroctonus ponderosae*; Pearson correlation of -0.8). For these species, the occurrence records used for the SDMs may not reflect the climatic niche represented by the physiological thresholds obtained from laboratory studies. For other species, we observed a good spatial match between the two approaches regarding distribution ranges (e.g. *Spodoptera litura*; Pearson correlation of 0.88), suggesting that the occurrence records for these species well represent their fundamental climatic niche, giving additional robustness to the prediction (Hijmans & Graham, 2006). For future investigations, we suggest using ensemble approaches of physiological models and SDMs for a proper understanding of the modelled system, as proposed in previous studies (Overmars, de Groot & Huigen, 2007). One approach could be to restrict the predicted distribution from correlative SDMs with the fundamental niche produced by physiological models (Kearney & Porter 2009). Physiological models alone are too general, predicting only the fundamental climatic niche, while SDMs may be too restricting, capturing non-accountable factors (e.g. restriction through competition), which distort model projections to future conditions (Sinclair, White and Newell, 2010). However, physiological models give a more direct biological understanding than statistical models, which can be more valuable than exact prediction (Lobell & Asseng, 2017).

Our results suggest that climate change will lead to an accelerated increase in pest pressure over large parts of Europe in the near future. We observed a non-linear relationship between niche limit positions and the prevalence of insect pest species. Crossing the inflection point implies a transition from cold- to warm-adapted species, and crossing the breakpoint temperature of 0°C of minimum temperature of the coldest month implies an abrupt increase in the number of pests with suitable climatic conditions and therefore in the number of pest species that may threaten European crop production. Previous studies have shown that climate change will entail northward movement of insect pest species in the near future (Bebber et al., 2013; Grünig et al., 2020). Here, we identified an inflection point around -3°C in the minimum temperature of the coldest month, beyond which the number of pest species with suitable climatic conditions in Europe accelerates.

Finding an inflection point for the minimum temperature of the coldest month below 0°C would be reasonable, given the physiology of insects and their reaction to freezing. Cold tolerance limits the distribution of many insects that do not go through winter diapause (Bale & Hayward, 2010). As we considered only monthly mean temperatures, the temperatures actually experienced by insects are likely to be more extreme than those reported here. For a monthly minimum temperature around -3°C, freezing events are very likely to occur, even in microhabitats that potentially buffer air temperature fluctuations and provide shelter to insects for overwintering (Danks, 1978). Minimum temperature and freezing events are known to act as limiting factors for insect spreading and protect many regions from invasions (Maxmen, 2013; Jarosik et al., 2015), underlining the importance of the inflection point.

Based on the non-linear response of pest niche distributions along a temperature gradient, we investigated the temporal and spatial dynamics of inflection points under climate change. We showed that the presence of two groups of species, warm-adapted and cold-adapted, could lead to two waves of increasing pest pressure. While northern regions are currently facing the first wave of insect pest invasion, with the cluster of cold-adapted species, Southern and Central European regions have already passed the inflection point temperatures, and are therefore expected to face the second wave, with the cluster of warm-adapted species, in the near future. The expected timing of the arrival of the second wave in these regions depends on the RCP scenario. Our results support the findings of previous studies, showing that abating

CO2 emissions could be crucial in preventing the impact of pests on crop yields (Deutsch et al., 2018), as we find a greater number of species with suitable climatic conditions under the RCP8.5 scenario than under RCP4.5. Moreover, our results show that some areas are already confronted with increased pest pressure, including most parts of Southern Europe, the British Isles and Western Europe. Indeed, these regions serve regularly as entry gates to Europe for invasive crop pests, such as Drosophila suzukii (Calabria et al., 2012) and Tuta absoluta (Desneux et al., 2010). France and Italy have the highest recorded numbers of established alien invertebrates in Europe (Roques et al., 2009). While these countries are part of the major pathways of global trade and entry gates to Europe for international shipping traffic, the Mediterranean climate has mild winters, supporting the establishment of more species than in northern regions. These findings support the importance of border control and improved inspection capacity with increasing trading volume (Poland & Rassati 2019).

The analyses applied in our study have limitations arising from data availability and differences in the total number of species for which suitable models could be developed depending on the modelling approach. Including data on more detailed requirements for insect development (e.g. on diapause initiation and termination) would improve the individual physiological models, however such data is scarce and not available for a broad range of species. Further, the size of the sample influences the outcome of the general response of species prevalence with respect to temperature. We tried to circumvent this problem by including data for a wide range of pests, including both cold- and warm-adapted species, but our list of pests is not complete. In addition, the global species pool for invasive insects shows no sign of saturation (Seebens et al., 2017). Indeed, quarantine (i.e. potentially invasive) species were underrepresented in this study, suggesting an even stronger acceleration of pest pressure after the inflection point is crossed. We observed that the inferred inflection zones for pests are very similar, irrespective of the chosen modelling approach and despite the fact that different sets of species were included in the analysis (75 species with physiological models and 159 with SDMs). We checked whether the same pattern occurs with only a subset of the species by only using the 53 species for which we could develop models for both the deductive and the inductive approach. The results confirmed the existence of an inflection point around -3°C. Within the warm-adapted cluster, the majority are quarantine species, implying a high invasion risk in new areas if minimum temperatures exceed the inflection point in these regions. Established pest species, for which we also predicted range shifts towards higher latitudes and expanding areas with suitable climatic conditions within Europe, heighten pest pressure in these regions.

Increasing temperatures will not only promote more invasions of quarantine pests, but also increase the spread of established pests, threatening agricultural cropping areas that are expanding to more northern latitudes in response to global warming.

Conclusions

We used deductive and inductive models to highlight trends of increasing climate suitability for insect pest species across Europe and a non-linear distribution of their climatic niches along a minimum temperature gradient. We found good model agreement between physiological models and SDMs under current climatic conditions. Forecasts under climate change showed diverging model agreement for pest species over time, indicating increasing uncertainty. Further, investigating the non-linear relationship between pest prevalence and minimum temperature made it possible to identify an inflection point beyond which the number of pest species with suitable climatic conditions increases rapidly. By mapping the inflection temperature spatially, we showed temporal and spatial dynamics of potential pest pressure under future climate change. Such information can inform policy-makers and stakeholders on where and when climatic conditions approach the transition point for the onset of accelerated pest invasions. New insights are necessary for planning crop protection strategies that can effectively help control the new threats. Ultimately, with expanding areas in Europe becoming susceptible to pest pressure in the near future, we advise a strengthening of surveillance measures in general and border control in particular, and for an improvement in inspection capacity.

Data Sharing and Accessibility statement

The data and code that support the findings of this study are available from the corresponding author upon reasonable request.

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Author contributions

M.G. contributed to conceiving ideas, gathering distribution data, establishing and running models, performing analysis and writing the manuscript; D.M. contributed to conceiving ideas and writing; P.C contributed to conceiving ideas, performing analysis and writing; L.P. contributed to conceiving ideas, establishing models and writing. All authors gave final approval for publication.

Supplementary Material

Note S1: Variable selection procedure

We modelled all species using two variables: minimum temperature of the coldest month and growing degree days above 5°C. We investigated model performance with area under the ROC-plot curve (AUC) and true skill statistics (TSS) values, as well as visual inspection of the projections. For species not reaching acceptable performance, we tested the models using second-order polynomials and later also using one of the two variables alone or in combination with monthly maximum temperature. As a result, for 23 crops and 24 pest species we used growing degree days as a single predictor variable, for two crop species we used maximum temperature as a single predictor variable, and for two pest species we used maximum temperature in combination with growing degree days. For eight pest species we used minimum temperature and maximum temperature as predictor variables. All species with the variables used for their models are listed in Table S1.

Supplementary Figures

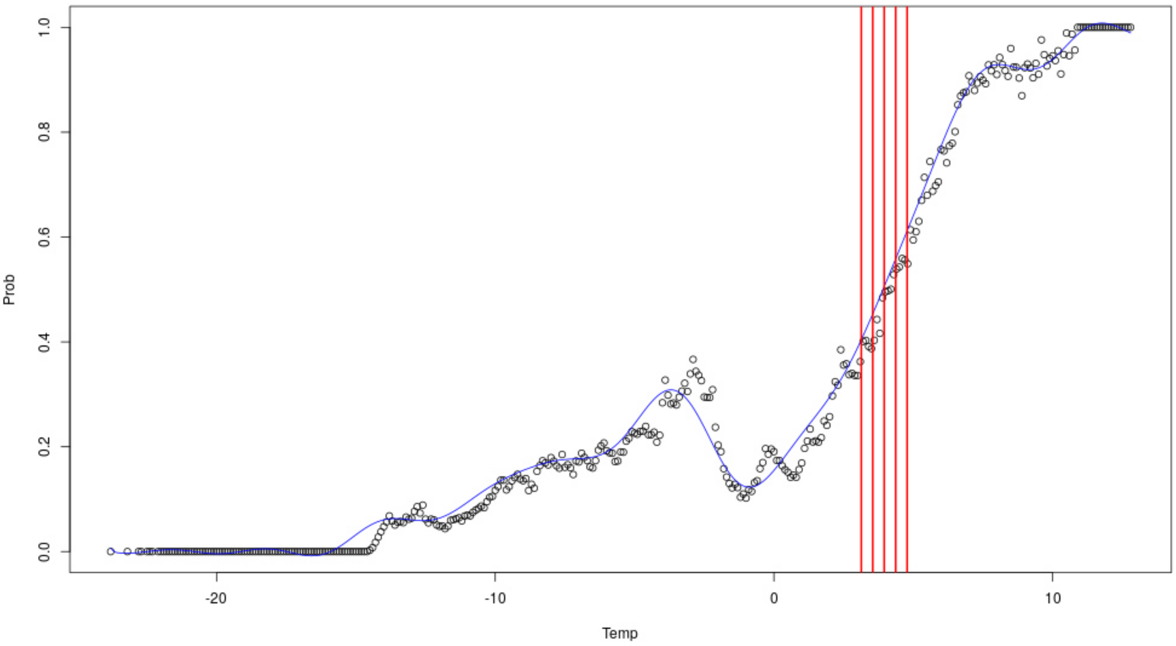


Figure S1: Schematic display of the method used to find the turning point for each species. The blue line represents the fitted GAM and the red lines indicate the temperatures of the turning points for all thresholds between 0.4 and 0.6 in steps of 0.05.

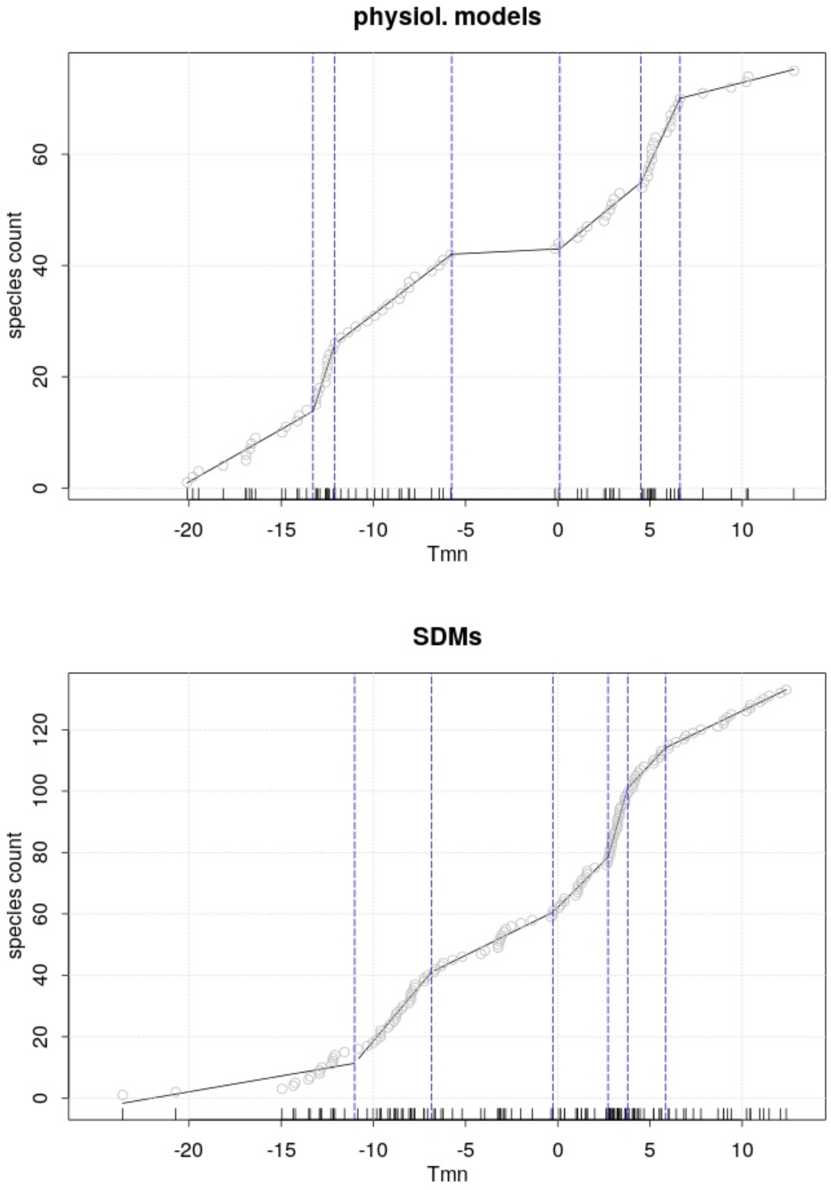


Figure S2: Analysis using the ‘segmented’ package in R to identify breakpoints in the distribution of turning points. The upper panel shows results for physiological models, and the lower panel shows results for SDMs.

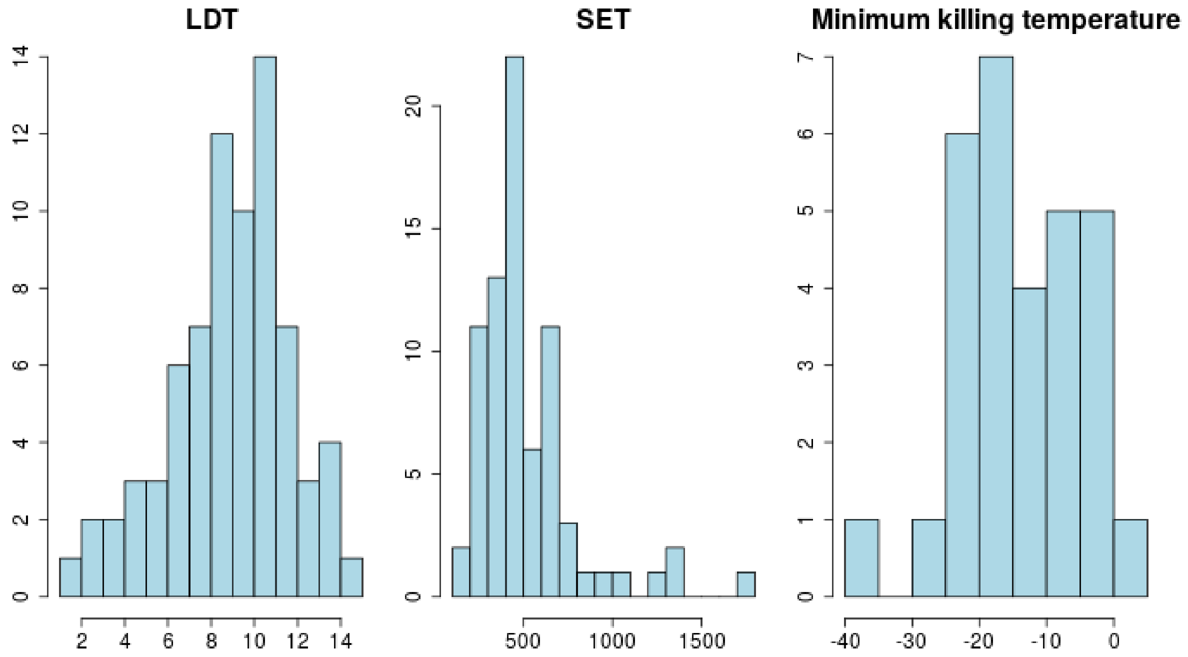
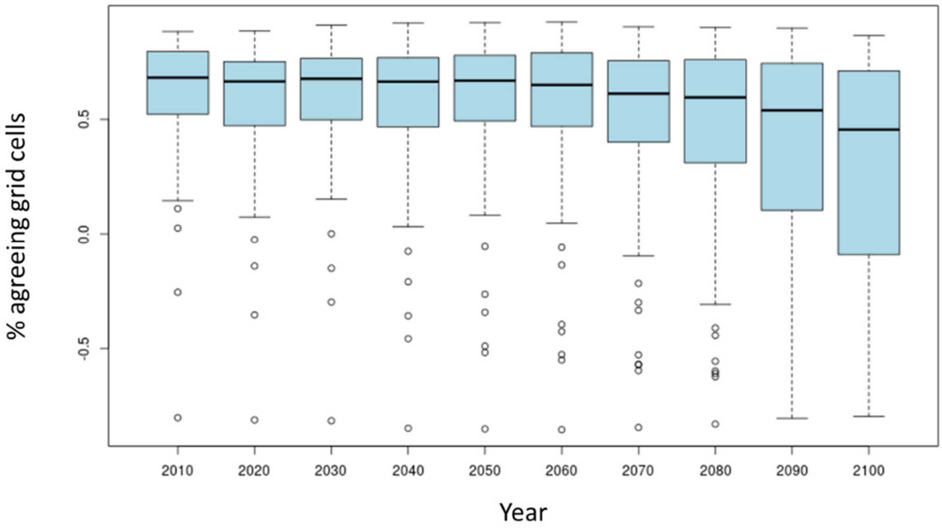


Figure S3: Histograms of species development thresholds used in the study. We could not obtain data on minimum killing temperature ($T_{kill,min}$) for all species, and this variable therefore contains a smaller number of data points than lower development threshold (LDT) and sum of effective temperatures (SET), i.e. the number of growing degree days (GDD) above the LDT required for the completion of a generation.



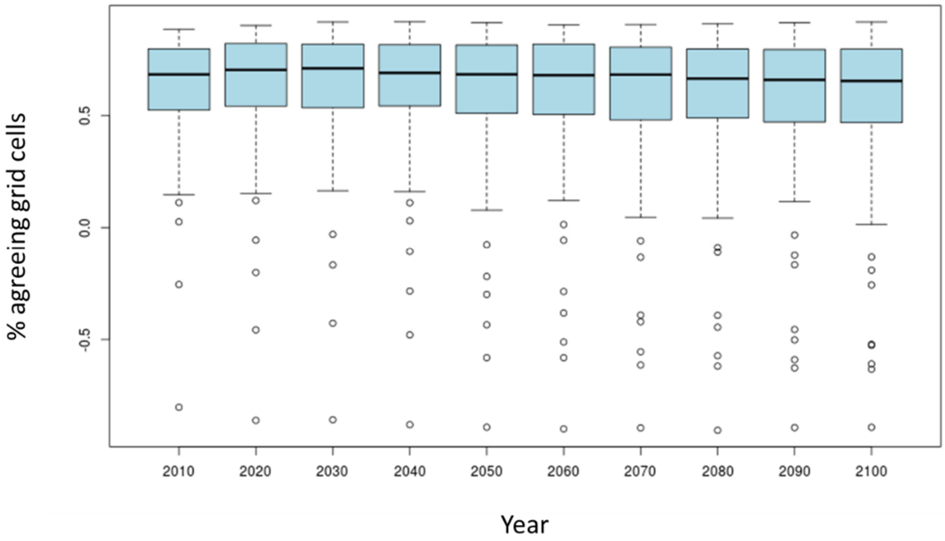
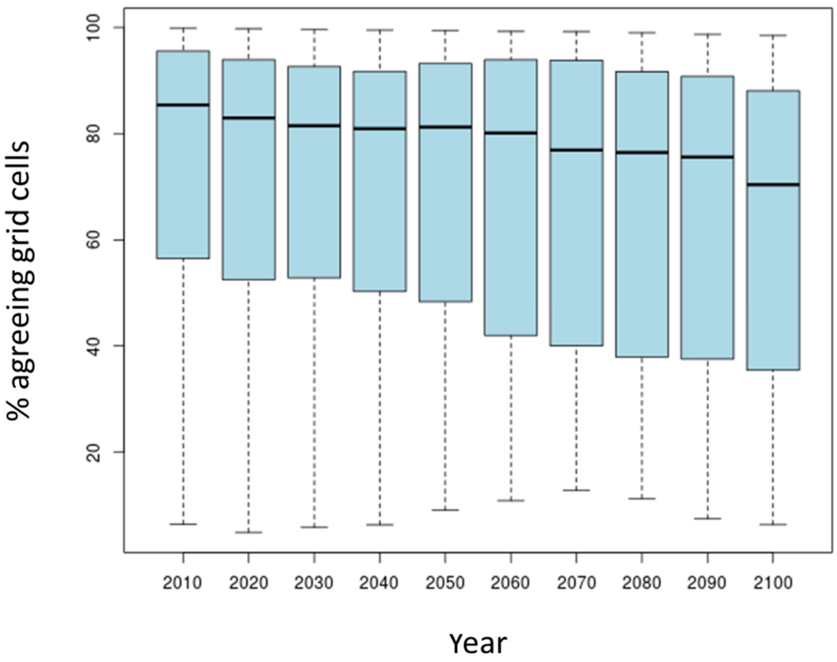


Figure S5: Median of model agreement as Pearson correlation of suitability indices over time, with RCP8.5 in the upper panel and RCP4.5 in the lower panel.



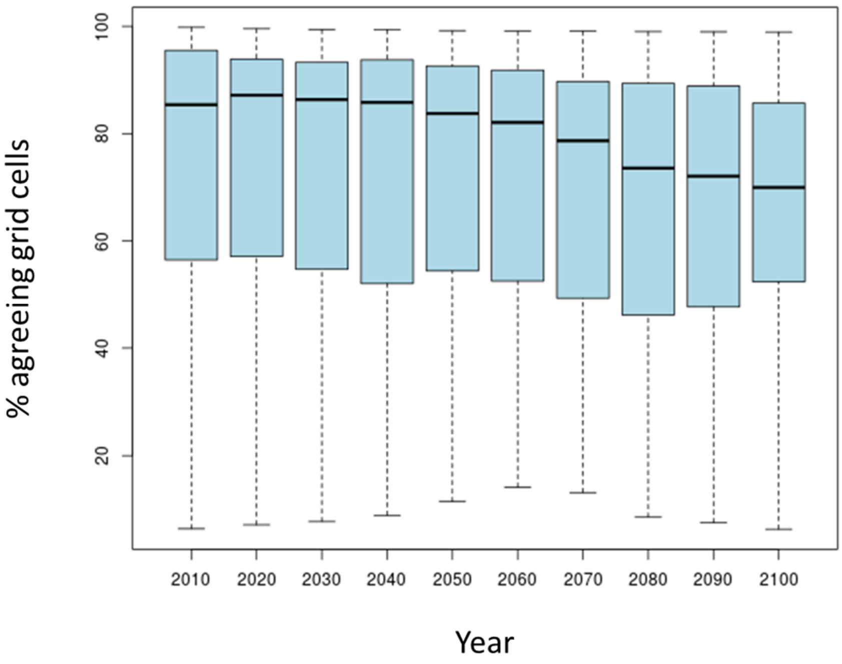


Figure S6: Median of model agreement as percentage of agreeing grid cells over time, with RCP8.5 in the upper panel andRCP4.5 in the lower panel.

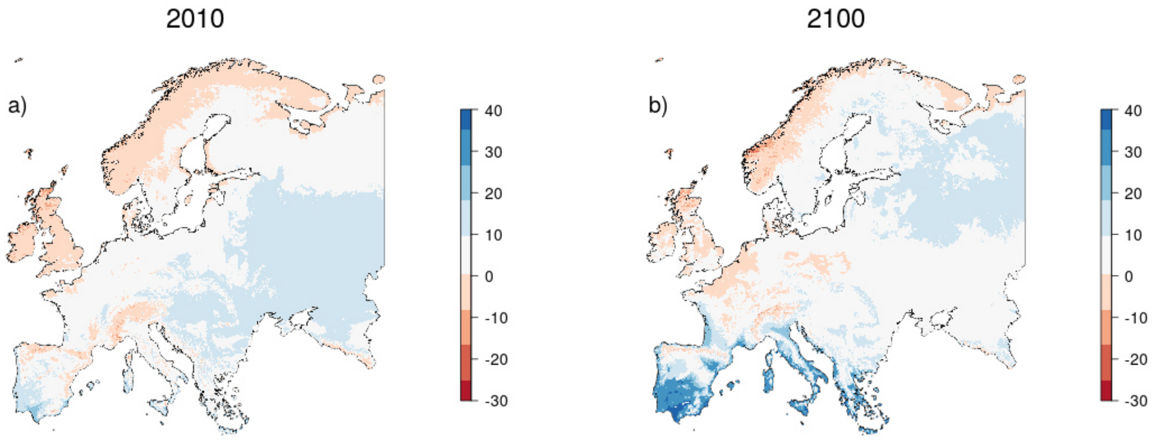


Figure S6: Absolute model disagreement between physiological models and SDMs under the RCP8.5 climate change scenario. We subtracted the raster layer of the SDM projection from the raster layer of the physiological model projection, and summed up the resulting layers of all species. Red areas show where SDMs predict more species occurrence than physiological models, and blue areas vice versa. The panels show disagreement (a) for pests in 2010, (b) for pests in 2100, (c) for crops in 2010, and (d) for crops in 2100.

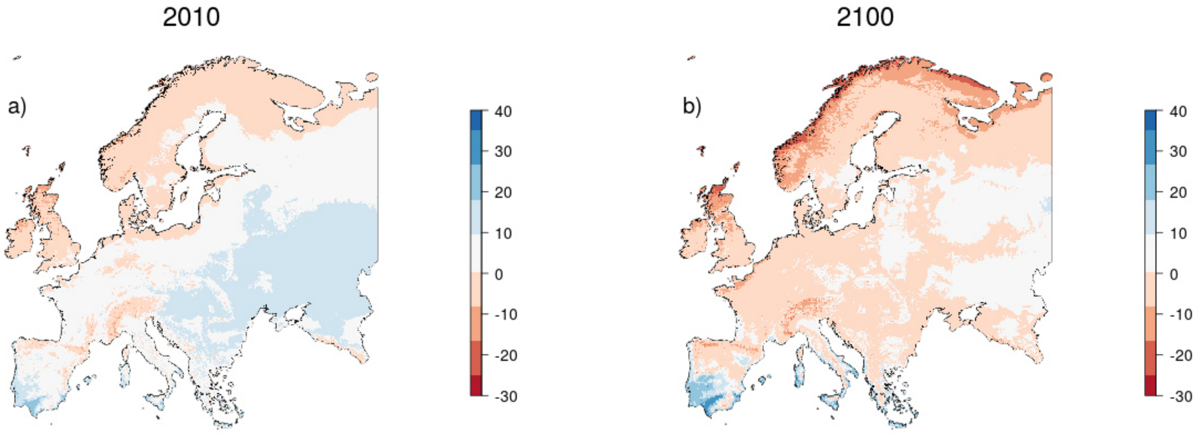


Figure S7: Same as Figure S6 but for climate change scenario RCP4.5.

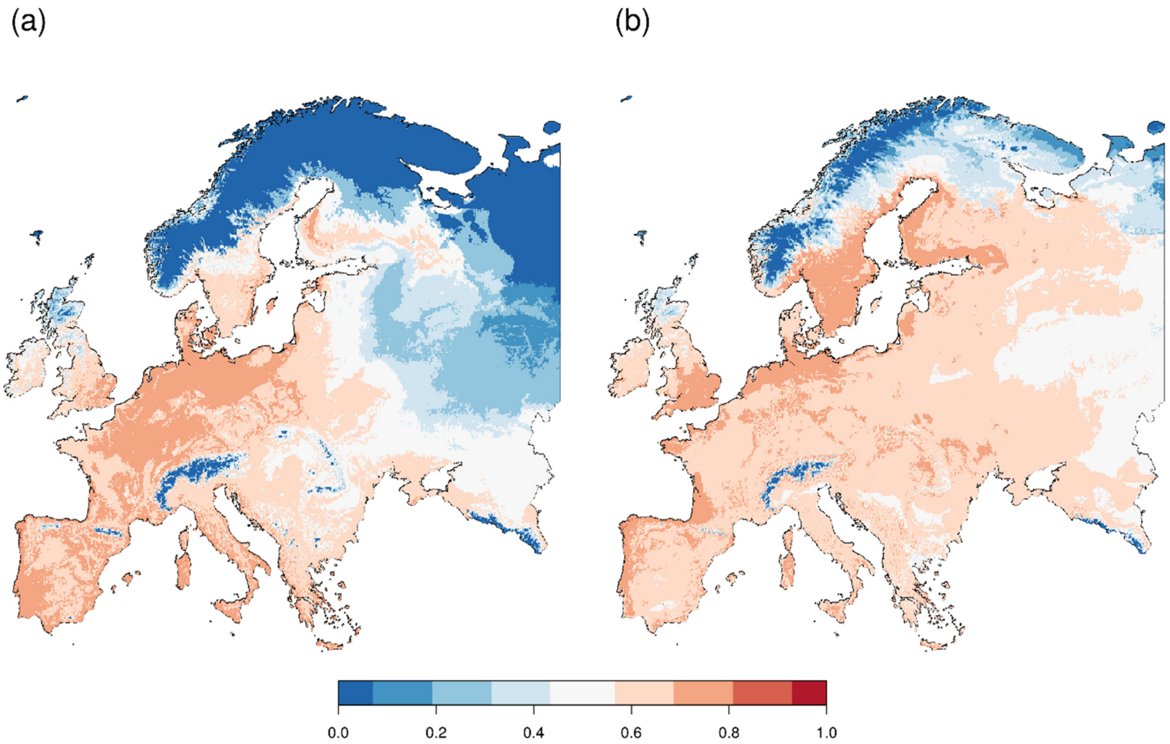


Figure S8: Maps of model agreement (Sorensen similarity index) for 2010 (a) and 2100 (b). Blue/red colours indicate lower/higher community similarity of predicted species. Results in (b) are based on the RCP4.5 climate change scenario (for results based on the RCP8.5 scenario, see Figure 1).

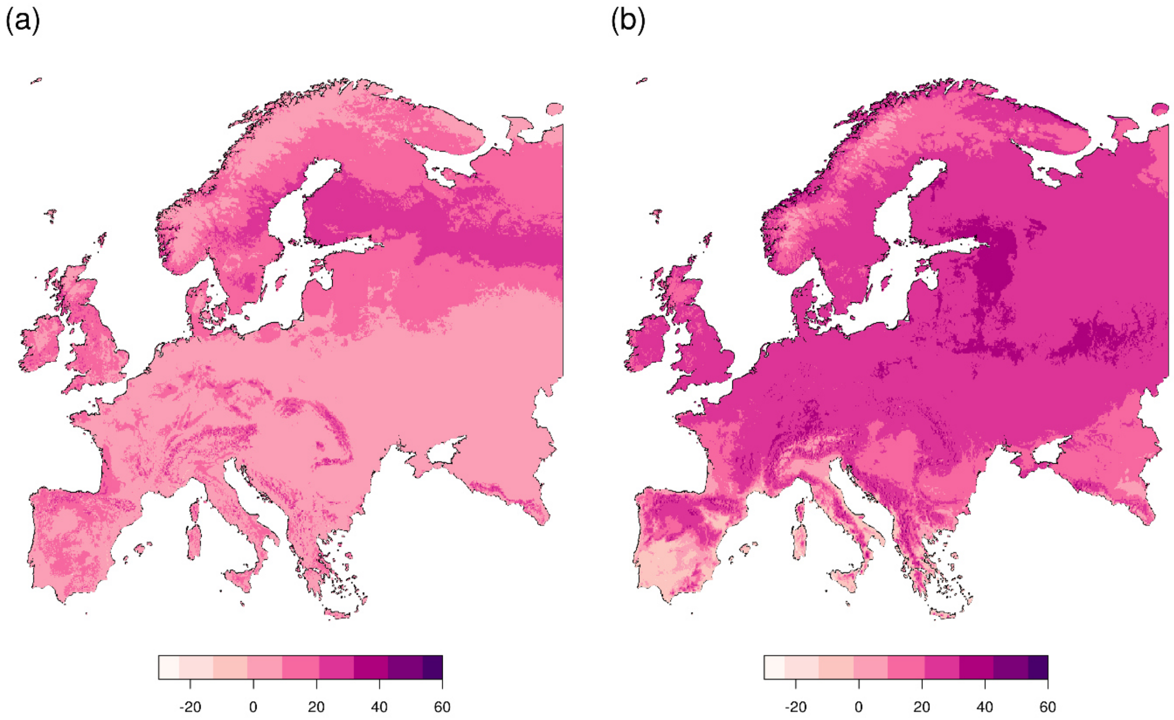


Figure S9: Same as Figure 3 but for RCP4.5.

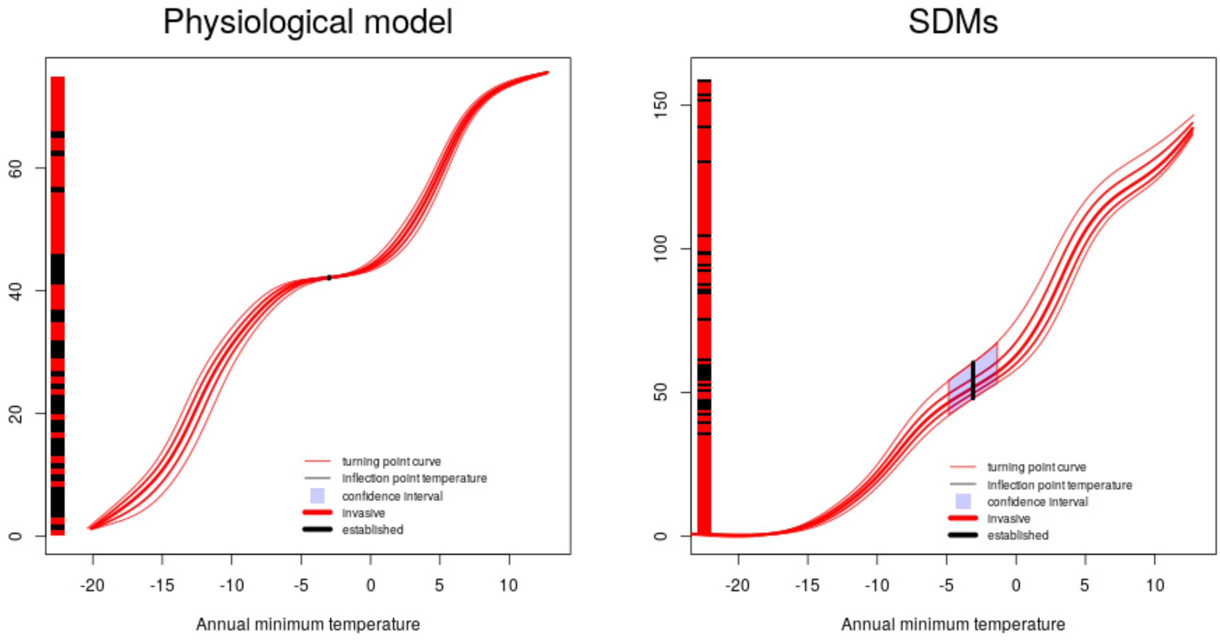


Figure S10: Turning-point lines for the five different cut-off thresholds (red lines). The blue polygon indicates the inflection zone, including the median (black lines). Red and black marks on the left side of the graphs show the category of pests: invasive (red) or established (black).

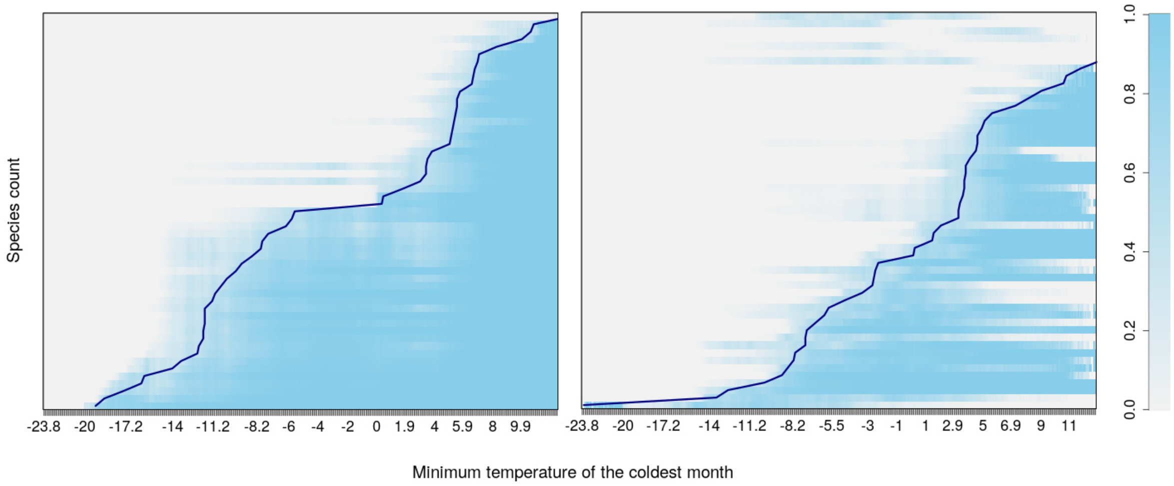


Figure S11: Same as Figure 3 but for the subset of 53 species for each modelling approach.

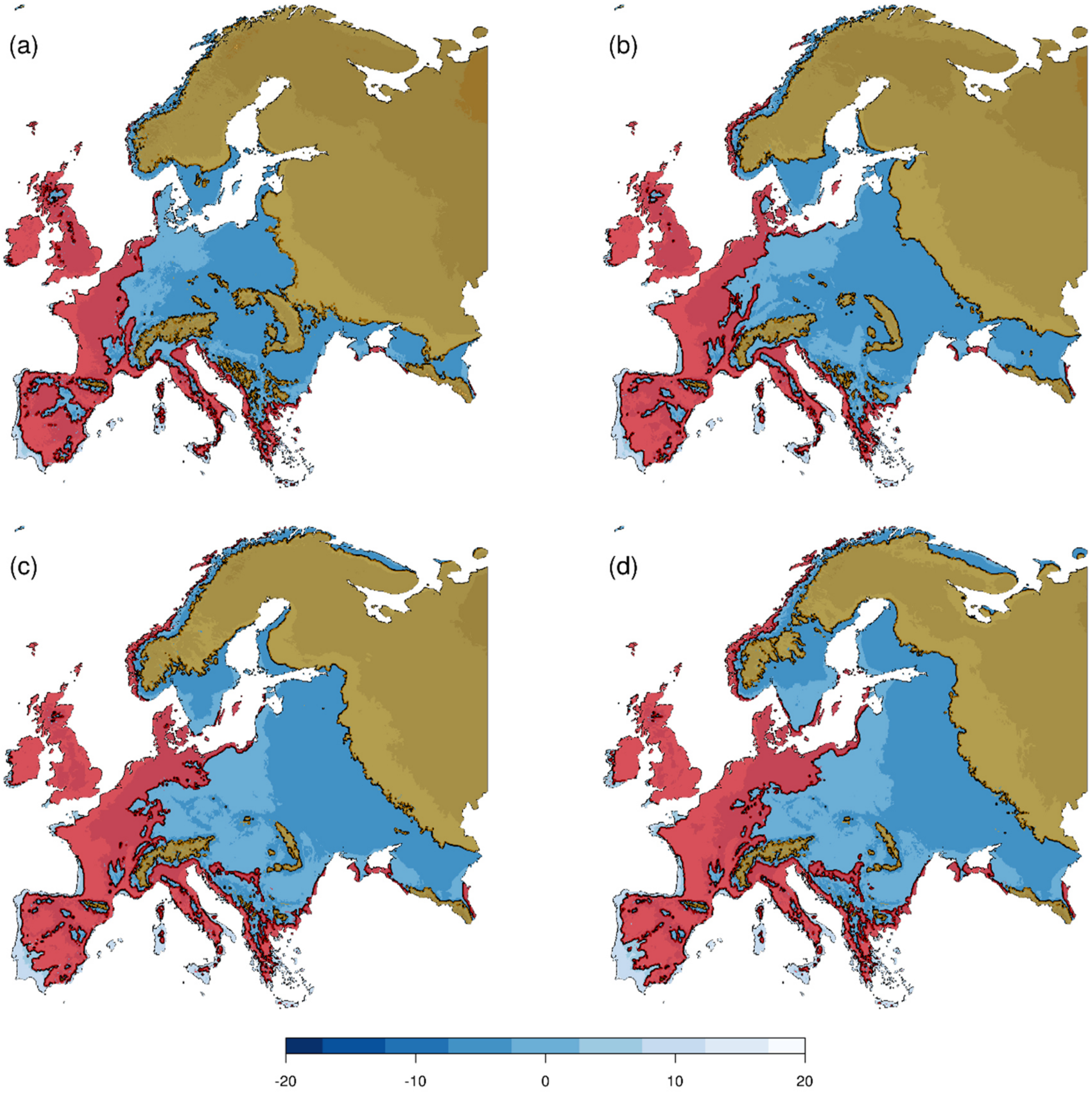


Figure S12: Same as Figure 4 but for physiological models.

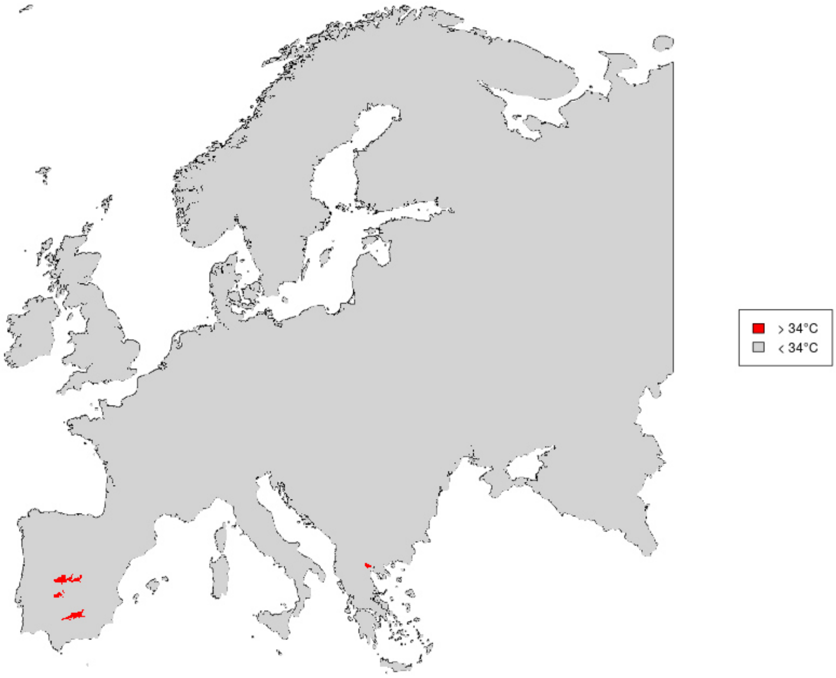


Figure S13: Areas predicted to reach a monthly mean temperature of more than 34°C in 2100 in one or more months (red). Values were calculated as the mean of the four GCMs in the RCP8.5 scenario.

Supplementary tables

Table S1: List of pest species modelled with physiological models. Quarantine species are indicated with the value 1, established species with the value 0.

Species	**Quarantine/Established**
Acrolepiopsis assectella	0
Adoxophyes orana	0
Aleurocanthus woglumi	1
Anarsia lineatella	0
Anastrepha fraterculus	1
Anastrepha ludens	1
Anoplophora glabripennis	1
Anthonomus grandis	1
Anthonomus signatus	1
Bactrocera cucurbitae	1
Bactrocera dorsalis	1
Bactrocera latifrons	1
Bactrocera tryoni	1
Bactrocera zonata	1
Baris lepidii	1
Bemisia tabaci	0
Cacoecimorpha pronubana	0
Cacopsylla pyricola	0
Carposina sasakii	1
Ceratitis capitata	1
Ceratitis rosa	1
Choristoneura occidentalis	1
Choristoneura rosaceana	1
Thaumatotibia leucotreta	1
Cydia pomonella	0
Delia antiqua	0
Delia platura	0
Dendroctonus ponderosae	1
Diabrotica virgifera virgifera	1
Diaphorina citri	1
Diuraphis noxia	0
Euwallacea fornicatus	1
Frankliniella occidentalis	1
Grapholitha molesta	0
Halyomorpha halys	0
Helicoverpa armigera	1
Helicoverpa zea	1
Hyphantria cunea	0
Ips calligraphus	1
Ips cembrae	0
Ips typographus	0
Leptinotarsa decemlineata	1
Leucoptera malifoliella	0
Liriomyza bryoniae	0

Liriomyza huidobrensis	1
Liriomyza sativae	1
Liriomyza trifolii	1
Lobesia botrana	0
Lycorma delicatula	1
Lymantria dispar	0
Mayetiola destructor	0
Neoleucinodes elegantalis	1
Orgyia pseudotsugata	1
Ostrinia nubilalis	0
Oulema melanopus	0
Pectinophora gossypiella	0
Phthorimaea operculella	0
Phyllotreta cruciferae	0
Pieris brassicae	0
Popilia japonica	1
Psacothea hilaris	0
Pseudaulacaspis pentagona	0
Rhagoletis cerasi	0
Rhagoletis indifferens	1
Rhagoletis pomonella	1
Scirtothrips dorsalis	1
Spodoptera eridania	1
Spodoptera frugiperda	1
Spodoptera littoralis	1
Spodoptera litura	1
Stephanitis takeyai	0
Tecia solanivora	1
Thrips palmi	1
Toxoptera citricida	0
Tuta absoluta	1

Table S2: List of pest species modelled with species distribution models (SDMs). Variables used for the SDMs for each species are shown. Quarantine species are indicated with the value 1, established species with the value 0.

Species	Quarantine/Established	Variable 1	Variable 2
Acrolepiopsis assectella	0	GDD	MinTemp
Aleurocanthus woglumi	1	GDD	MinTemp
Aleurodicus dispersus	1	GDD	MinTemp
Amyelois transitella	1	GDD	MinTemp
Anastrepha fraterculus	1	GDD	MaxTemp
Anastrepha ludens	1	GDD	MinTemp
Anastrepha obliqua	1	GDD	MinTemp
Anoplophora chinensis	1	GDD	MinTemp
Anoplophora glabripennis	1	GDD	MinTemp
Anthonomus bisignifer	1	GDD	MinTemp
Anthonomus grandis	1	GDD	MinTemp
Anthonomus signatus	1	GDD	NA
Argyrotaenia velutinana	1	GDD	MinTemp
Aroga trialbamaculella	1	GDD	MinTemp
Arvelius albopunctatus	1	GDD	MinTemp
Bactericera cockerelli	1	GDD	MinTemp
Bactrocera carambolae	1	GDD	NA
Bactrocera cucurbitae	1	GDD	MinTemp
Bactrocera latifrons	1	GDD	MaxTemp
Bactrocera occipitalis	1	GDD	NA
Bactrocera tryoni	1	GDD	MinTemp
Bemisia tabaci	0	GDD	MinTemp
Cacoecimorpha pronubana	0	GDD	MinTemp
Cactoblastis cactorum	1	GDD	MinTemp
Cameraria ohridella	0	GDD	MinTemp
Carposina sasakii	1	GDD	MinTemp
Ceratitis capitata	1	GDD	NA
Ceratitis cosyra	1	GDD	MinTemp
Ceratitis quinaria	1	MinTemp	MaxTemp
Ceratitis rosa	1	GDD	NA
Ceroplastes sinensis	0	MinTemp	MaxTemp
Chinavia marginata	1	MinTemp	MaxTemp
Chloridea virescens	1	GDD	MinTemp
Chlorochroa sayi	1	GDD	MinTemp
Choristoneura occidentalis	1	GDD	MinTemp
Choristoneura rosaceana	1	GDD	MinTemp
Chrysodeixis eriosoma	1	GDD	MinTemp
Cingilia catenaria	1	GDD	MinTemp
Conotrachelus nenuphar	1	GDD	NA
Coscinoptycha improbana	1	GDD	MinTemp
Cotinis nitida	1	GDD	MinTemp
Cydia pomonella	0	GDD	MinTemp
Dacus ciliatus	1	GDD	MinTemp
Daktulosphaira vitifoliae	0	GDD	NA
Delia antiqua	0	GDD	MinTemp

Dendroctonus ponderosae	1	GDD	MinTemp
Diabrotica barberi	1	GDD	NA
Diabrotica speciosa	1	GDD	MinTemp
Diabrotica undecimpunctata howardi	1	GDD	NA
Diabrotica undecimpunctata undecimpunctata	1	GDD	MinTemp
Diabrotica virgifera virgifera	0	GDD	MinTemp
Diabrotica virgifera zeae	0	GDD	MinTemp
Diaphorina citri	1	GDD	MinTemp
Diaprepes abbreviatus	1	GDD	MinTemp
Diuraphis noxia	0	GDD	MinTemp
Drosophila suzukii	0	GDD	MinTemp
Dryocosmus kuriphilus	0	GDD	MinTemp
Egira curialis	1	MinTemp	MaxTemp
Epicauta abadona	1	GDD	MinTemp
Epicauta immaculata	1	GDD	MinTemp
Epicauta occidentalis	1	GDD	MinTemp
Epicauta vittata	1	GDD	MinTemp
Epiglaea apiata	1	GDD	MinTemp
Epilachna vigintioctopunctata	1	GDD	MinTemp
Epitrix cucumeris	1	GDD	MinTemp
Erthesina fullo	1	GDD	MinTemp
Eudocima fullonia	1	GDD	MinTemp
Euschistus conspersus	1	GDD	MinTemp
Euschistus servus	1	GDD	MinTemp
Euwallacea fornicatus	1	GDD	MinTemp
Frankliniella occidentalis	0	GDD	NA
Grapholita packardi	1	GDD	MinTemp
Grapholitha molesta	0	GDD	MinTemp
Halyomorpha halys	0	GDD	MinTemp
Helicoverpa armigera	0	GDD	MinTemp
Helicoverpa assulta	1	MinTemp	MaxTemp
Helicoverpa punctigera	1	GDD	NA
Helicoverpa zea	1	GDD	MinTemp
Heteronychus arator	1	GDD	MinTemp
Homalodisca vitripennis	1	GDD	MinTemp
Ips typographus	0	GDD	MinTemp
Lacanobia subjuncta	1	GDD	MinTemp
Lamprolonchaea brouniana	1	GDD	MinTemp
Leptinotarsa decemlineata	1	GDD	MinTemp
Leptoglossus zonatus	1	GDD	MinTemp
Leucinodes cordalis	1	GDD	MinTemp
Leucinodes orbonalis	1	GDD	MinTemp
Limonius californicus	1	GDD	MinTemp
Lineodes integra	1	GDD	MinTemp
Liriomyza bryoniae	0	GDD	NA
Liriomyza huidobrensis	0	GDD	NA
Liriomyza sativae	1	GDD	MinTemp
Liriomyza trifolii	0	GDD	MinTemp
Lissorhoptrus oryzophilus	1	GDD	MinTemp
Listronotus bonariensis	1	GDD	NA

Lobesia botrana	0	GDD	MinTemp
Lobiopa insularis	1	GDD	MinTemp
Lycorma delicatula	1	GDD	MinTemp
Lygus elisus	1	GDD	MinTemp
Lygus hesperus	1	GDD	NA
Lygus lineolaris	1	GDD	MinTemp
Lygus shulli	1	GDD	MinTemp
Lymantria dispar	0	GDD	MinTemp
Maconellicoccus hirsutus	1	GDD	MinTemp
Malacosoma americana	1	GDD	MinTemp
Manduca sexta	1	GDD	MinTemp
Megacopta cribraria	1	GDD	MinTemp
Melanotus communis	1	GDD	MinTemp
Metamasius hemipterus	1	GDD	MinTemp
Naupactus leucoloma	1	GDD	MinTemp
Neoceratitis cyanescens	1	MinTemp	MaxTemp
Nipaecoccus viridis	1	GDD	MinTemp
Nysius huttoni	0	GDD	MinTemp
Ochropleura implecta	1	GDD	MinTemp
Oemona hirta	1	GDD	NA
Opogona sacchari	1	GDD	NA
Orgyia pseudotsugata	1	GDD	MinTemp
Orthosia hibisci	1	GDD	MinTemp
Paralobesia viteana	1	GDD	NA
Phlyctinus callosus	1	GDD	NA
Phthia picta	1	GDD	MinTemp
Phyllotreta cruciferae	0	GDD	MinTemp
Phyrdenus divergens	1	GDD	MinTemp
Platynota flavedana	1	GDD	MinTemp
Platynota idaeusalis	1	GDD	MinTemp
Platynota stultana	1	GDD	MinTemp
Popilia japonica	1	GDD	MinTemp
Popillia japonica	1	GDD	MinTemp
Psacothea hilaris	0	GDD	MinTemp
Rhagoletis cerasi	0	GDD	MinTemp
Rhagoletis cingulata	0	GDD	MinTemp
Rhagoletis completa	0	GDD	MinTemp
Rhagoletis fausta	1	GDD	MinTemp
Rhagoletis indifferens	1	GDD	MinTemp
Rhagoletis pomonella	1	GDD	MinTemp
Rhagoletis suavis	1	GDD	MinTemp
Saperda candida	1	GDD	MinTemp
Scirtothrips dorsalis	1	GDD	MinTemp
Sparganothis sulfureana	1	GDD	MinTemp
Spodoptera albula	1	GDD	NA
Spodoptera eridania	1	GDD	NA
Spodoptera frugiperda	1	GDD	MinTemp
Spodoptera latifascia	1	GDD	NA
Spodoptera littoralis	1	GDD	NA
Spodoptera litura	1	GDD	MinTemp
Spodoptera ornithogalli	1	GDD	MinTemp

Spodoptera praefica	1	GDD	MinTemp
Strauzia longipennis	1	GDD	MinTemp
Systena frontalis	1	GDD	MinTemp
Thaumatotibia leucotreta	1	GDD	MinTemp
Thrips imaginis	1	GDD	MinTemp
Thrips palmi	1	GDD	MinTemp
Trichoferus campestris	1	GDD	MinTemp
Trioza erytreae	1	GDD	NA
Tuta absoluta	1	GDD	MinTemp
Unaspis citri	1	GDD	MinTemp
Xylena nupera	1	GDD	MinTemp
Zaprionus indianus	1	GDD	MinTemp
Zonosemata electa	1	GDD	MinTemp

CHAPTER II

CHAPTER III

Applying deep neural networks to predict incidence and phenology of plant pests and diseases

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Abstract

A major challenge of agriculture is to improve the sustainability of food production systems in order to provide enough food for a growing human population. Pests and pathogens cause vast yield losses, while crop protection practices raise environmental and human health concerns. Decision support systems provide detailed information on optimal timing and necessity of crop protection interventions, but are often based on phenology models that are time-, cost- and labour-intensive in development. Here, we aim to develop a data-driven approach for pest damage forecasting, relying on big data and deep learning algorithms. We present a framework for the development of deep neural networks for pest and pathogen damage classification and show their potential for predicting the phenology of damages. As a case study, we investigate the phenology of the pear leaf blister moth (*Leucoptera malifoliella*, Costa). We employ a set of 52,322 pictures taken during a period of 19 weeks and establish deep neural networks to categorize the images into six main damage classes. Classification tools achieved good performance scores overall, with differences between the classes indicating that the performance of deep neural networks depends on the similarity to other damages and the number of training images. The reconstructed damage phenology of the pear leaf blister moth matches mine counts in the field. We further develop statistical models to reconstruct the phenology of damages with meteorological data and find good agreement with degree-day models. Hence, our study indicates a yet underexploited potential for data-driven approaches to enhance the versatility and cost-efficiency of plant pest and disease forecasting.

Keywords: Decision support system; deep neural network; image classification; insect pest; phenological modelling.

Introduction

Agriculture is facing major challenges concerning food security and food production for a global human population predicted to grow to nine billion by 2050 (Godfray et al., 2010). Besides shifting towards more plant-based diets and decreasing food waste (Shepon et al. 2018; West et al. 2014), sustainable intensification is necessary for food and environmental security (Godfray et al., 2010; Garnett and Godfray, 2012). The rapidly growing field of precision agriculture uses modern information technology, including computer vision and artificial intelligence, provides enormous potential to contribute to the goals of more sustainable agriculture (Bongiovanni and Lowenberg-deBoer, 2004; Lindblom et al. 2017; Patricio and Rieder, 2018). Referred to as “smart farming”, technological development is foreseen to support a more efficient use of natural resources and better target plant protection from pests and pathogens while minimizing hazards to environmental and human health (Chakraborty and Newton, 2011; Tilman et al. 2011; Garnett et al. 2013; Walter et al., 2017). Pests and pathogens are responsible for large yield losses (Oerke, 2006), and are often counteracted with pesticides (Lamichhane et al. 2015). Raising concerns regarding the negative externalities of pesticides on human health and environmental safety (Geiger et al. 2010; Tegtmeier and Duffy 2004, Pimentel and Burgess, 2014) foster strategies to reduce the risks from their use without compromising productivity and profitability (Lechenet et al., 2017). Reliable pest and pathogen detection and prediction support more timely and precise interventions, and thus reduced pesticide use.

Machine learning has great potential to assist the development of innovative methods for pest and pathogen management, supporting more sustainable plant protection (Behmann et al., 2015). The identification of pest and pathogens and the detection of damages on crops are challenging for farmers, yet crucial for the decision on appropriate control measures (Martinelli et al., 2015; Lamichhane et al., 2016). Deep neural networks (DNNs) and algorithms for image classification (Goodfellow et al., 2016) can serve the detection of pests and pathogens for plant protection (e.g. Mohanty et al. 2016; Sladojevic et al. 2016; Ferentinos 2018). For example, convolutional neural networks (CNNs; Krizhevsky et al., 2012; Szegedy et al., 2015) have been used to identify different pathogens on apple leaves, based on image data (Liu et al. 2018; Zhong and Zhao 2020), and for the classification of insect pest species occurring on crops (Cheng et al., 2017; Thenmozhi & Reddy, 2019). The goal of these technological implementations is to help growers to recognize and detect pests and pathogens in the field, fostering faster and more self-reliant evaluation of the pest situation in situ and support decision-making processes to optimize yields in a sustainable way (e.g. Sladojevic et al. 2016). Appropriate timing of pesticide applications is not trivial (Tang et al., 2010) and anticipating the damage can improve application precision. Temporal precision of pesticide application can increase the efficacy and reduce the number of required applications, and therefore lower the total amount (Möhring et al., 2020). Therefore, advancing novel technologies may lead to faster and more efficient recognition processes and eventually contribute to decrease risks associated to pesticide use, as well as yield losses.

Decision support systems (DSS) assist crop producers with the surveillance, decision on optimal timing and anticipation for the need of pesticide applications (Samietz et al. 2007) and big data in combination with deep learning can increase the precision of DSS. In general, DSS for pests and pathogens rely on phenological models, where the timing of crucial events in the life-cycle of those damaging organisms, measured under controlled temperature conditions, are coupled with meteorological data to predict their seasonal occurrence. Phenological models have reached good performances for the prediction of pest and pathogen occurrence, offering an effective complement to field observations (e.g. Schaub et al. 2017), but are still time- and cost- intensive in development. Resulting models often target specific pest-crop or pathogen-crop systems, are location-dependent (Donatelli et al., 2017) and rarely updated once established. In the meantime, the life cycles of many insects are altered by changing climate conditions (Kingsolver et al. 2011). With warming climate, phenological shifts and disruption of synchrony between host plants and pests are widespread reactions (Forrest, 2016). This leads to increasing discrepancies between model predictions and actual observations, because forecast models at the core of DSS are seldom reparametrized to account for altered insect biology. Further, climate change promotes the introduction and spread of invasive species into newly suitable, so far uncolonized regions (Bebber et al. 2013; Grünig et al., 2020), requiring fast development of new DSS. Novel technologies to analyze big data based on deep learning (LeCun, 2015) can support monitoring and deliver the baseline for developing phenological models needed, in combination with weather data and forecasts, to anticipate pest damages.

Using 52,322 photographs taken under field and standard conditions during the spring-summer of 2019, here we develop a framework toward pest phenology forecasting based on big data and deep learning algorithms. We focus on a proof of concept for the development of damage classification tools, which, in combination with meteorological data, are used to produce phenological models (Figure 1). We use DNNs to classify damages on apple tree leaves and investigate the phenology of six main classes of damages predicted by the DNNs. We couple the predicted occurrence of damages with meteorological data to model damage phenology. Our case study targets the apple crop because it is the most important fruit crop in Switzerland, with a production varying between 250,000 and 450,000 tons per year depending on weather (SBV, 2019). Concerning damages, the focus lays on the mines of the pear leaf blister moth (*Leucoptera malifoliella* Costa, Lepidoptera: Lyonetiidae; from here on blister moth), a pest that has recolonized orchards in central Switzerland since 2013 (Zwahlen et al., 2017). The blister moth prefers apple trees as host plants and in case of heavy infestation can affect the photosynthesis and cause premature leaf drop (Ivanov, 1976; www.cabi.org). Larvae of the blister moth are solitary miners producing characteristic brown, round mines that are distinguishable from physical damages. Our working hypotheses are as follows:

1. We expect that the development of DNNs to categorize different classes of damages on apple leaves is feasible with a subset of the 52,332 images collected during one season.
2. We expect that by applying the resulting classification tools to the full dataset, we can reconstruct the phenology of blister moth mines, which should match conventional monitoring methods.
3. We expect to find a meteorological signature in damage phenology of the blister moth, providing the basis for the development of statistical prediction models.

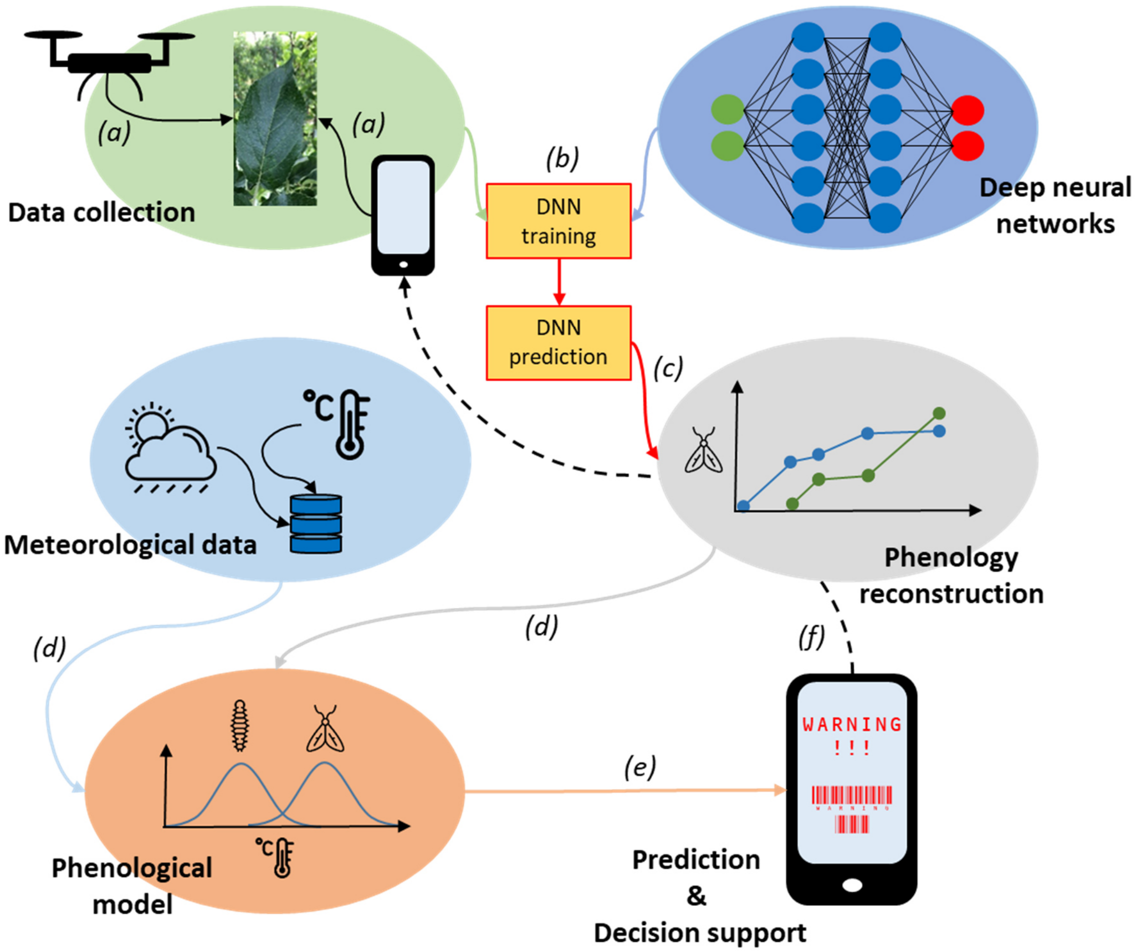

Figure 1: Conceptual figure showing the overall goal of the framework for developing pest damage forecasting tools. Data collection can be implemented with drones or citizen science approaches (a). The collected data can be used to train deep neural networks (DNN) for image classification to recognize pest and pathogen damages (b). Once the classification tool is established, predictions using deep neural networks can be used for reconstructing the phenology of pest damages (c). Coupling damage phenology with meteorological data enables establishing phenology models (d). Eventually, these phenology models can be used for predictions and in DSS, aiming at informing on pest occurrence to support growers and experts, for instance by implementing the tool in a smartphone app (e). Image classification tools can then reinforce the data collection, by making it available to citizen scientists (f). In this study, we focus on the deep learning and phenology modelling aspects within this framework.

Methods

Data collection

We sampled leaves and collected images weekly between April 15th and August 28th 2019 in three apple orchards in central Switzerland, in Kleinwangen (47°11'49.3"N; 8°17'22.8"E; 536 m a.s.l.), Gelfingen (47°13'12.9"N; 8°16'10.0"E ; 557 m a.s.l.) and Waedenswil (47°13'18.4"N; 8°40'38.6"E; 483 m a.s.l.; see Figure S1 for map with the locations). Using smartphone cameras, we collected pictures of leaves in the field (from here on referred to as field pictures) and sampled leaves to take pictures under standardized conditions in the lab (from here on standardized pictures). Taking pictures using smartphones results in pictures of a similar quality expected if they were taken by growers, untrained citizen scientists or from automated devices such as drones. We conducted a structural sampling in the three orchards. In each location, we sampled at least 400 leaves per week. With this structural sampling, we aimed to capture a representative set of pest symptoms. As the orchards have different number of trees planted in a different number of rows, we conducted three different sampling strategies. In Kleinwangen and Gelfingen, we took two pictures from every third, respectively fourth tree per row. In Waedenswil we took four pictures from every tree. Field pictures and leaves were taken from the lower part and upper part of the trees. Collected leaves were kept in a 3°C storage room before we took pictures under standardized conditions. We used scotch tape to stick the leaves on a white paper in order to have a uniform background. The pictures were taken with one of two different mobile phones, an iPhone 6 (8 megapixel camera) and a Sony Xperia X (23 megapixel camera). At the time of sampling, in Kleinwangen and Gelfingen extension services were conducting tests on the efficacy of pesticides targeted against blister moth. We distinguished between treated and untreated sections of the orchards for the image data collection, irrespective of the management of the treated trees.

In parallel to the leaf and picture sampling, population density of blister moth was monitored with pheromone trapping and mine counting in Gelfingen. The orchard was exposed to testing of eight different control methods including a control section. We placed one trap (*Delta-trap* pheromone traps, Andermatt Biocontrol AG, Grossdietwil, Switzerland) in the control section to document the occurrence of adults on a weekly basis. Weekly, 50 randomly selected leaves per treatment section were inspected visually for the presence of mines, resulting in 400 leaves per week. Each leaf was carefully checked by eye and the occurrence of mines was noted. We registered the total number of mines per 50 leaves.

Meteorological data

Meteorological data were extracted from the gridded dataset (2 km x 2 km) obtained from the Swiss Federal Office of Meteorology and Climatology (MeteoSwiss; meteoswiss.admin.ch). Daily data were extracted for the year 2019 and aggregated to the weekly resolution in order to match the weekly sampling rate of the damage monitoring. The statistical models employed to create the gridded data are described in Ceppi et al. (2010) and Frei (2014) (daily minimum, maximum and mean temperature), Frei and Isotta (2019) precipitation and Dürr and Zelenka. (2009) (solar radiation). To track phenology, we further calculated the accumulated temperature sum (i.e. degree-days) as the cumulative sum of the mean temperature over 5°C on daily basis.

Data preparation

In total, we gathered 52,322 pictures of apple leaves. We manually classified 8,735 randomly sampled standardized and field pictures into damage classes. We found 42 classes, including classes containing combined damages and classes with a low number of pictures (less than 100). We focused on seven classes with at least 100 pictures for further processing (Figure 2):

- *Undamaged*: no damages detected on the leaf.
- *PLBM*: mines of blister moth detected;
- *Physical damages*: holes, cracks, fissures or deformations;
- *Brown spots*: brownish spots distinguishable from blister moth mines;
- *Lepidoptera*: rolled in leaf edges indicating pupae of Lepidoptera species;
- *Mildew*: powdery mildew (Podosphaera leucotricha) detected;
- *Feeding*: feeding damage from herbivore insects

We cropped all images to an extent of 2840 x 1560 pixels in the centre of the image to focus on the leaf rather than the background (e.g. Figure 2 left-most pictures of class *Undamaged*).

Deep neural networks

We used DNNs to apply image classification of the entire image in order to allocate it to one out of several classes. We implemented our deep neural network approach in R (version 3.5.3; R Core Team, 2019), using the R-package 'reticulate' (version 1.13.0-9003; Ushey, Allaire & Tang, 2019) to open an interface to python. We used 'Keras' (version 2.2.5.0; Allaire & Chollet, 2019) and 'Tensorflow' (version 1.9; Allaire & Tang, 2019) R-packages as DNN frameworks. We loaded image data with the *image_data_generator* function of the 'Keras' R-package. Images were imported and resized to 256 x 256 pixels with three channels (i.e. RGB colour channels) and rescaled to values between 0 and 1. Further, we applied data augmentation to the training dataset during the image import. Data augmentation is a common strategy to increase the number of images in the training dataset. We applied the following specifications in the *image_data_generator* function to augment the data: zooming (range = 0.4), rotations (range = 90), width and height shifts (range = 0.2), shearing (range = 0.2), horizontal and vertical flips. As network structure we used the ResNet50 (He et al. 2016) model, loaded with weights pre-trained on ImageNet (Deng et al. 2009) as base for our model architecture. We fine-tuned all layers of the ResNet50 network and added one dense layer with 256 nodes and a *ReLU* activation function, as well as an output layer with a softmax activation function on top of the ResNet50 to adapt to our dataset. Moreover, we added dropout (0.5) after the ResNet50 network and as well after the densely connected layer to prevent model overfitting. Further, we used an *RMSprop* optimizer with a base learning rate of 0.0001 and a decay of 0.00001 for gradient descent. We set the mini-batch size, which defines how many images the DNN takes into account per step for calculating the model error and updating the model coefficients, to 32. All networks were trained for 100 epochs (i.e. iterations over the full training dataset).

We trained DNNs on different combinations of classes (i.e. different classification tasks). First, we trained DNNs for each damage class to distinguish images of this class, from all other images (i.e. all other classes as one summary class), resulting in six classification tasks. Second, we trained full model DNNs to classify the six main classes (*PLBM, Undamaged, Physical damages, Brown spots, Lepidoptera* and *Mildew*) simultaneously in one DNN. In a preliminary analysis step, we used *Feeding* and *Physical damages* as independent classes, but compounded them for the final analysis because DNNs struggled with differentiating these two classes. We trained DNNs for the same classification tasks with field pictures. To establish DNNs, we split the categorized images of each class into five subsets for a 5-fold cross-validation. DNNs were trained on four subsets (80% of the data) and tested on the left out subset (20%). From the 80% training data, 20% were used for validation to tune hyperparameters (i.e. settings to control the learning process of a deep neural network). This procedure was repeated five times resulting in five different DNNs per classification task. We measured the performance of DNNs for each classification task on the test set with F1-score averaged over the five DNNs per classification task. F1-scores (equation 1) were calculated with the scores for true positives (TP), false positives (FP) and false negatives (FN), resulting in values ranging from 0 to 1, 1 being perfect classification:

$$\boldsymbol{F1} = \frac{\boldsymbol{TP}}{(\boldsymbol{TP}+\mathbf{0.5}*(\boldsymbol{FP}+\boldsymbol{FN}))} \tag{1}$$

Additionally, we measured performance with classification accuracy as the percentage of correctly classified images. DNNs were evaluated with the performance on the test data set, which was not included in the construction of the network.

Coupling pest damage with meteorological data

We used DNNs to classify all images from Kleinwangen and Gelfingen, because in these two locations we found blister moths. We used the *predict_class* and the *predict_proba* function of the 'Keras' R-package (version 2.2.5.0; Allaire & Chollet, 2019) to obtain predictions on the class and the pseudo-probabilities per class for all images using the full model DNNs. The pseudo-probability prediction are output scores from DNNs showing how confident the DNN is in predicting a class for an image. We grouped the predictions into locations and dates. Further, we calculated the percentages of damaged leaves per sampling event, scaling the number of damaged leaves of each class with the total number of collected leaves to correct for uneven sampling, as the sampling events did not result in the exact same number of images. We used GLMs to model the percentage of damaged leaves with weekly meteorological data as predictor variables. Climatic variables included growing degree-days (i.e. cumulative sum of mean temperature over base temperature of 5°C), mean temperature, precipitation, solar radiation and diurnal temperature range. We ran GLMs for each meteorological predictor, and one multivariate GLM with all predictors, allowing second-degree polynomials and assuming binomial error distribution. We used the *ecospat.adj.D2.glm* function of the 'ecospat' R-package (version 3.0; Broennimann et al., 2018) to obtain model deviance as adjusted D2 values of all models. Additionally, we use the *glarma* function of the 'glarma' R-package (version 1.6-0, Dunsmuir & Scott, 2015) to run GLARMA (Generalized Linear Autoregressive Moving Average) models for the same predictor variables, to check whether accounting for temporal autocorrelation would change the model estimation of parameters.

Results

Data collection

We collected 52,322 pictures of apple tree leaves in total over 19 weeks of sampling. 35,903 pictures were taken in the field and 21,087 under standardized conditions. For the two locations, where we used the image data to reconstruct the blister moth phenology, we gathered 14,466 images in Gelfingen and 18,384 in Kleinwangen. We did not find different signals from the different treatments and therefore only present the results for the collection of treated and control section. From the 8,735 categorized pictures, we found that class *PLBM* contained 1,390 images, *Undamaged* 1,415, *Physical damages* 1,139, *Brown spots* 2,025, *Lepidoptera* 103 and *Mildew* 134 images.

Deep neural networks

We established DNNs for 14 different classification tasks of apple tree leaves. F1-scores for classification tasks of standardized pictures ranged from 0.69 to 0.93 with the exception of the class *Lepidoptera* (0.32), where the number of training images was very low (with a total of 103 manually classified images, for model training we used between 26 and 44 images depending on classification task (standardized or field) and the cross-validation chunk). Classification accuracy ranged from 91.3% to 99.5%. The full model including all six classes reached a F1-score of 0.89 (standard deviation across the five cross-validation runs: ± 0.035) and a classification accuracy of 95.4% (± 1.5%). DNNs performed generally more poorly on images taken in the field (Figure 2). F1-scores for field pictures ranged from 0.52 to 0.90 with the exception of *Physical damage* where no F1-score could be determined because none of the test images was assigned to *Physical damages*, meaning that this class was not recognized by the DNN based on field pictures. Classification accuracy for all classes ranged from 87.5% to 99.4%. The full model reached a F1-score of 0.85 (± 0.02) and a classification accuracy of 87.7 % (± 1.6 %) for field images.

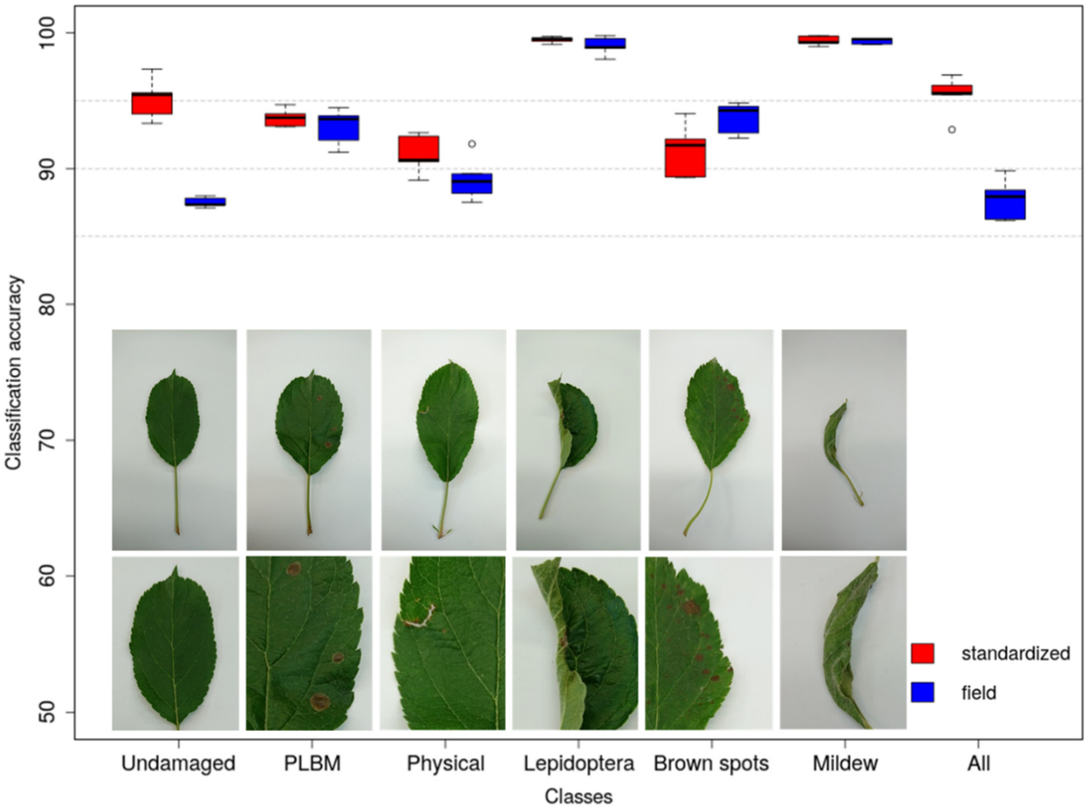

Figure 2: DNN performance for the 14 classification tasks measured as classification accuracy. Boxes show the classification accuracy variation over the 5-fold cross validation. Red boxes show the results for standardized pictures, blue boxes for field pictures. For the results of F1-scores see Figure S2. Grey dashed lines mark the 85%, 90% and 95% lines. Images show the different classes considered in the study. F.l.t.r: *Undamaged, PLBM, Physical damage, Lepidoptera, Brown spots, Mildew*. Right-most boxes show the performance of the full model.

We used the trained DNNs to classify the images of the dataset that were not categorized a priori. From the five DNNs trained for the cross-validation for the full model we selected the one with the best performance. With the full model for standardized pictures, we found 7,627 images of class *PLBM*, 5,598 *Undamaged*, 3,063 *Physical damages*, 156 *Brown spots*, 122 *Lepidoptera* and 850 *Mildew*. The full model for field pictures resulted in a prediction of 7,350 *PLBM*, 10,638 *Undamaged*, 899 *Physical damages*, 131 *Brown spots*, 282 *Lepidoptera* and 693 *Mildew*. The full model for field images was unable to detect the class *Lepidoptera* (see Figure S2 & Figure S3 for reconstructed phenologies of all damage classes). We used the DNNs to reconstruct the phenology of the blister moth (Figure 3). We found very similar patterns for the two locations, with an increase of blister moth mines in mid-June and a first peak in early July. Standardized and field pictures show very similar results, although field pictures indicated the peak one week later than the standardized pictures.

Although we found different DNN performance for the standardized pictures and the field pictures, predictions to the full dataset resulted in very similar patterns of the phenology of the different damage classes. Further, we compared the blister moth phenology predictions of the DNNs with count data of blister moth adults in traps and mines obtained from surveys in the same orchards (Fig. 4). The count data supports our findings for the blister moth phenology based on the predictions of DNNs. The phenology of the trapped adults explained patterns of the mines, which start to emerge 3 to 4 weeks after the peak of a generation of adults. These results matched well with literature descriptions of development times for one generation (e.g. 36 days at 18°C; Sáringer et al., 1985). We also observed the same pattern of decreasing numbers of mines in early to mid-July, which is explained by the simultaneous emergence of new leaves and the gap between the first and the second generation of blister moth larvae. Mine counts and reconstructed mine phenology showed a Pearson correlation coefficient between 0.938 and 0.978 for both locations with standardized and field pictures.

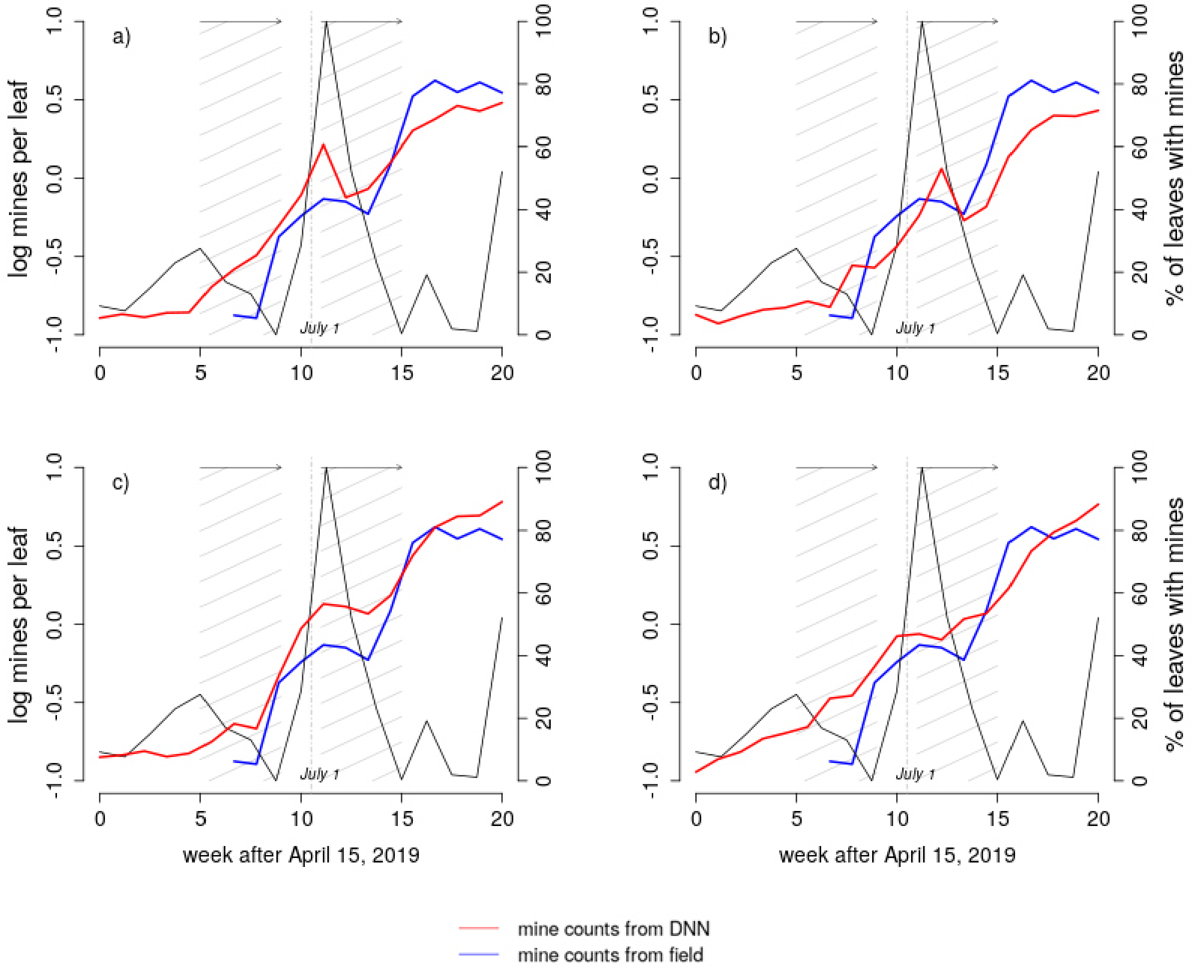

Figure 3: Comparison between blister moth mines phenology reconstructed with DNNs (red line) and count data of mines from the field (blue line). The black line marks the count data of adults caught in traps. The hatched areas in the background show a 4 week timespan between the peaks of the blister moth generations (adults) and the local peak of mines. Panels show the data for a) Gelfingen standardized pictures, b) Gelfingen field pictures, c) Kleinwangen standardized pictures, d) Kleinwangen field pictures.

Coupling pest damages with meteorological data

We quantified the relationship between the phenology of the blister moth and climate using GLMs (Figure 4). For both locations and for standardized and field pictures we found that degree-days is the most important variable, with adjusted D^2 values between 0.950 and 0.967 (Table 1). The full model explained only slightly more of the deviance ranging from 0.956 to 0.969. We found similar results with GLARMA models, confirming that degree-days is the best predictor for blister moth phenology from Gelfingen, but only the second best predictor for Kleinwangen after mean temperature (Table 2).

Table 1: Model deviance (as adjusted D2 values) for GLM on blister moth phenology with different meteorological predictor variables. Degree-days above 5°C (GDD), mean temperature (Tmean), precipitation (Precip), radiation (SRad), diurnal temperature (Diur) and the model with all predictors (Full).

	Gel. stand.	Kle, stand.	Gel. field	Kle. field
GDD	0.966	0.967	0.959	0.950
Tmean	0.841	0.767	0.773	0.804
Precip	0.006	0.014	0.032	0.018
Srad	0.332	0.287	0.286	0.317
Diur	0.202	0.176	0.211	0.194
Full	0.969	0.965	0.961	0.956

Table 2: Akaike's information criterion (AIC) for GLARMA models on blister moth phenology with different meteorological predictor variables. Degree-days above 5°C (GDD), mean temperature (Tmean), precipitation (Precip), radiation (SRad), diurnal temperature (Diur) and the model with all predictors (Full).

	Gel. stand.	Kle, stand.	Gel. field	Kle. field
GDD	344.6685	569.2	443.3927	534.1602
Tmean	346.8743	452.2735	504.6914	355.1499
Precip	2107.805	1949.889	2323.896	1555.169
Srad	448.142	592.8213	465.8917	396.9868
Diur	841.1444	795.4927	928.275	551.5733
Full	185.3556	233.9368	268.5195	227.7823

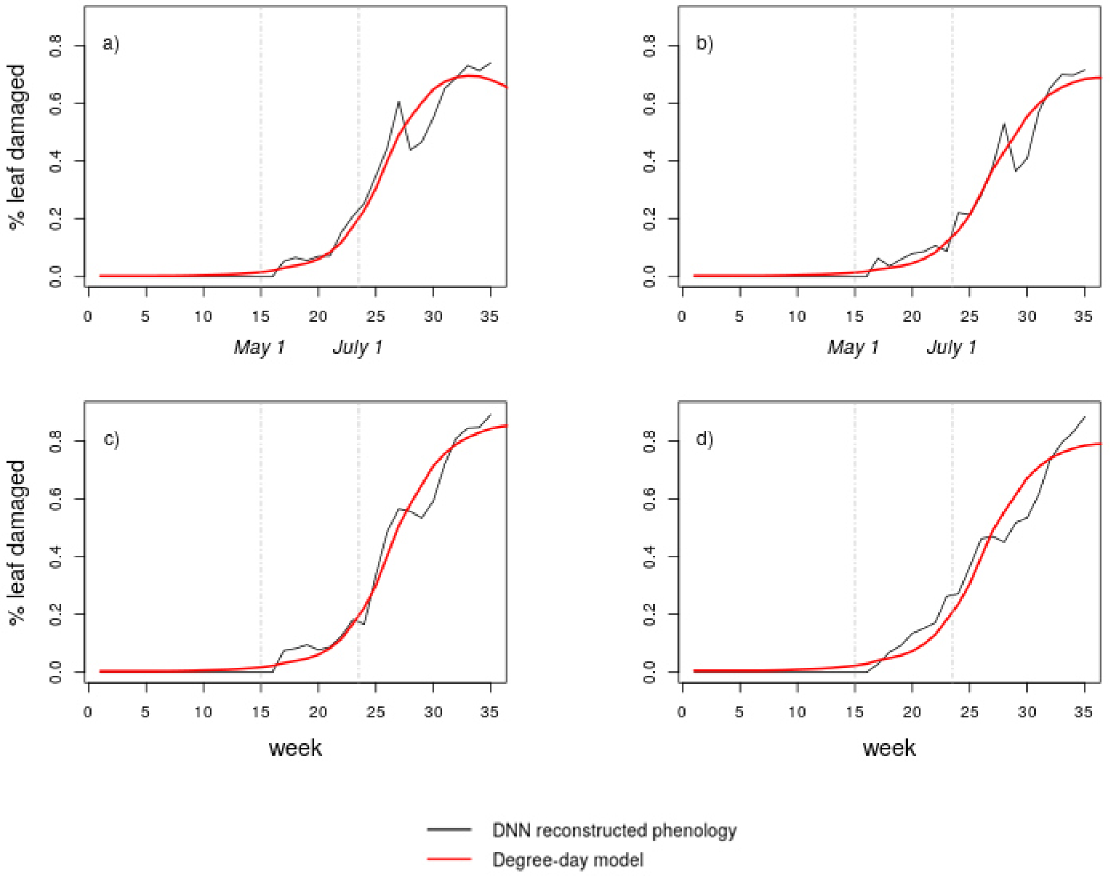

Figure 4: Comparison of the seasonal evolution of the inferred damage phenology (DNN) and the phenology modelled with GLMs. Panels show the data for a) Gelfingen standardized pictures, b) Gelfingen field pictures, c) Kleinwangen standardized pictures, d) Kleinwangen field pictures.

Discussion

In this study, we tested the feasibility of different segments of a framework for developing pest damage forecasting models, relying on big data, DNNs and meteorological data (Figure 1). Our case study on blister moth mines suggests that DNNs coupled with meteorological data are suitable tools for the proposed method. We use DNNs to build image classification tools to classify the damages of a large dataset of apple leaf images and to reconstruct the phenology of different damage classes (Figure S3). Using blister moth as a case study species, we show that the blister moth phenology predicted with DNNs matched count data of mines and adults in the field. Finally, we quantify the phenology of blister moth mines with meteorological variables and show that phenological models based on degree-days are well fitting the blister moth phenology. While we show here that, the proposed framework is feasible in principle, for the full implementation of the framework, data collection processes need to be optimized and the phenological models need to be validated with independent data.

Our results show that DNNs are suitable tools for pest damage classification based on image data, similarly as it has earlier been shown for other classification tasks (e.g. Mohanty et al., 2016; Cheng et al., 2017). Trained DNNs reached good model performance for categorizing blister moth damages with a classification accuracy of 93.8% (F1-score of 93.2); all other single class DNNs were trained successfully with F1-scores above 0.86 except *Physical damages* (0.69) and *Lepidoptera* (0.32) (see Figure S4 and S5 for some examples of misclassifications). In general, we observe better and more robust results for classes where more data for training were available. DNNs classifying multiple classes were struggling with distinguishing some of the classes, but performed well overall (F1-score of 0.89 for six classes). Compared to studies predicting several classes of pathogens, the accuracies of our DNNs are slightly lower (e.g. Oppenheim and Shani, 2017 reached 96% accuracy with five classes; see Barbedo, 2018 for an overview). A reason for this could be that the manually classified part of our dataset is rather small and applying a cross-validation lowers the number of pictures available to train the DNNs. In general, we observe that DNNs struggle with distinguishing between classes with similar symptoms, for example between *Physical damages* and *Feeding*, which we discriminated in preliminary analyses. Another reason for the decreasing model performance with more classes may lay in the co-occurrence of damages on one leaf, but general solutions to properly identify such simultaneous damages are still lacking (Barbedo, 2018). Further, we show that DNNs are also capable of classifying pest damages with images taken under field conditions (see results, section deep neural networks), which is crucial to develop useful pest or disease recognition tools, as the goal should be the application in the field (Sladojevic et al., 2016; Picon et al., 2019). Overall, DNNs established with field pictures show good results, but as expected, reach slightly lower performance than DNNs for standardized pictures, because external influences such as shading effects, multiple leaves, other plant parts or irrelevant objects in the background can be disturbing (Ferentinos, 2018). Particularly, DNNs struggled with the class of *Physical damages*. Still, the DNN for the class *PLBM* with field pictures reached a F1-score of 0.90 (classification accuracy of 93.1%). The full model DNN for field pictures was successful with an F1-score of 0.85 and classification accuracy of 87.7%. Our case study shows that the development of pest damage classification tools using DNNs is realizable, allowing to use those tools to obtain the phenology of classes by analyzing big datasets, given that sufficient data is available.

We highlight that reconstructing damage phenology with DNNs, coupled with meteorological data opens up new possibilities to produce phenological models for pest forecasting. Big data science has recently been proposed to help to overcome current limitations in pest forecasting (Orlandini et al. 2018). In our case study, we find that degree-days is the most important variable to model blister moth phenology. Degree-days have been shown to be a reliable predictor of insect development (e.g. Cayton et al. 2015) and are important components in phenology models for insects (Nietschke et al., 2007). This is important for the development of operational systems, as in many regions of the world temperature data are available at high spatial and temporal resolution. We validate the reconstructed phenology of the blister moth, with count data on adults and mines obtained from the same study sites, showing that classification tools are able to reconstruct the real phenology. Further, we show that our approach is suitable to reconstruct the phenology of other classes and therefore, could be used to investigate not only the phenology of insects, but also the phenology of other types of damages (e.g. *Mildew*). With sufficient image data, the prediction approach may also be implemented for pests and pathogens to find meteorological signals behind their seasonal occurrence or the occurrence of the entailed damages. Successful recognition tools for pathogens have already been developed (e.g. Fuentes et al., 2017; Liu et al. 2018) and seasonal occurrence of pathogens is often limited by abiotic factors (Rossi, Giosuè and Caffi, 2010). In addition, we emphasize that the framework for the establishment of this approach would also be suitable for invasive species phenology modelling, due to the potential of fast implementation. However, expert recommendations on management interventions need to be based on solid testing of control strategies by plant protection experts. Particularly for invasive species, this is crucial to implement sustainable control. We find promising results in this case study, underlining that the proposed framework could bring new opportunities for pest forecasting, given that new methods will help to overcome the lack of data availability.

While this case study highlights new possibilities for pest damage forecasting, we came across some limitations that need to be addressed in future studies. One of the main limitations is the low number of images of some classes we used to train the DNNs. Here, we use only a subset of our dataset where the frequency of the different classes is not equally distributed. This means that for some classes only few images are available for training and evaluation of a DNN.

Meanwhile, previous studies establish DNNs using the full data of large datasets (e.g. PlantVillage) for model training and evaluation (e.g. Mohanty et al., 2016). However, such image data is limited and previous studies in the field of plant disease classification often rely on the same dataset and similar tools, yielding in a low variation between the results of these studies (Barbedo, 2018; Arsenovic et al., 2019). Increasing the input data for DNNs could therefore promote higher robustness and performance of the classification tools of some classes (Sladojevic et al., 2016). Further, within our sampling period, the variation in meteorological conditions was rather small. Longer-term surveys are required to capture a broader scope of meteorological settings, leading to more robust phenological models. Similarly, data from long-term monitoring programs are needed to validate phenological models. With the implementation of new data collection strategies, these limitations may be overcome.

To address the limitations of the current work, as well as provide the base of the proposed framework for pest forecasting, innovative data collection strategies must be established. We present perspectives and potential approaches for acquisition of data for the proposed framework for pest damage forecasting. The main disadvantage of deep learning is the amount of data needed (Kamilaris & Prenafeta-Boldu, 2018) and not many agricultural image datasets are publicly available (Kamilaris et al. 2017; Arsenovic et al., 2019). To overcome this data scarcity, we propose two approaches for data collection. First, with the increasing number of smartphones used worldwide, allowing to record images, sound and location, there is a wide scope for gathering large datasets, in particular in the context of citizen science (Teacher et al. 2013). In agriculture, particularly in relation to pest and pathogen monitoring, there is pressing interest for this approach and farmers are traditionally interested in participating in research projects (Ryan et al., 2018). While citizen scientists benefit from the classification tool and the pest forecasting model, the collected image data can be used to create a feedback loop where new images can be used for updating the classification tool (see Figure 1). Additionally, an advantage of a citizen science approach could come from detection of new invasive species (Hulbert et al. 2017; Johnson et al., 2020), as famers might want to inform themselves and alert the responsible experts when they encounter a yet unknown damage. Finally, the acceptance for DSS is expected to be higher if users are involved in their development (Lynch, Gregor and Midmore, 2000).

The second approach we propose here is the implementation of drones (Floreano & Wood, 2015). Drones are expected to revolutionise precision agriculture by delivering big data that can be used for various purposes (Tripicchio et al., 2015; Finn and Donovan, 2016). For example, drones have been used for weed detection, irrigation equipment monitoring, or crop health monitoring (Veroustraete, 2015). Drones programmed with GIS inputs and equipped with high-resolution cameras (e.g. 15 megapixel, Shankar et al., 2018) are suitable tools to collect data in a structured way, which can be analysed with deep learning algorithms (Shankar et al., 2018). Together, these approaches highlight opportunities to overcome the lack of image datasets on pest and pathogens, allowing to advance with the proposed framework for pest forecasting and providing groundwork for other novel technologies supporting sustainable agriculture.

Conclusions

In conclusion, we present a framework for developing pest monitoring and forecasting tools that rely on big data and deep learning. A non-representative survey suggested that farmers are generally interested in the development of new forecasting tools, and that there is a demand for new technologies with broad applicability in plant protection. In this study, we focus on the segments of this framework connected to building DNNs and coupling the phenology reconstructed with those DNNs with meteorological variables to produce phenology models. The case study on blister moth phenology highlights that this approach is feasible. DNNs showed good performance on categorizing different classes of damages with pictures of leaves taken under standardized conditions and in the field. Further, the phenology of the blister moth obtained from DNNs matched the phenology observed with count data in the field well. While damage classification tools are valuable instruments for pest and pathogen monitoring, using those classification tools to reconstruct the damage phenology and coupling them with meteorological data, will promote new opportunities for early warning. Together, this study highlights that big data and modern technologies provide new opportunities to advance sustainable plant protection. To overcome the scarcity in data availability, which presents the main limiting factor for such data-driven approaches, here we suggest to address this issue with data collection based on citizen science or drones. Increasing data availability would not only support this framework for pest damage forecasting, but also foster further development towards applying modern information technology to tackle current agricultural challenges.

Code availability statement

The R codes for the models and calculations of the results and analysis are available from the corresponding author. The code and scripts will be published on a public repository upon manuscript acceptance.

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Author contributions

M.G. contributed to conceiving ideas, collecting image data and monitoring data, constructing and running deep neural networks, performing analysis and writing the manuscript; E. R. contributed to collecting image data and monitoring data; P. C. contributed to conceiving ideas, performing analysis and writing; D.M. contributed to conceiving ideas and writing; J. D. W. contributed to constructing deep neural networks and writing; L.P. contributed to conceiving ideas and writing. All authors gave final approval for publication.

Supplementary material

Supplementary Figures

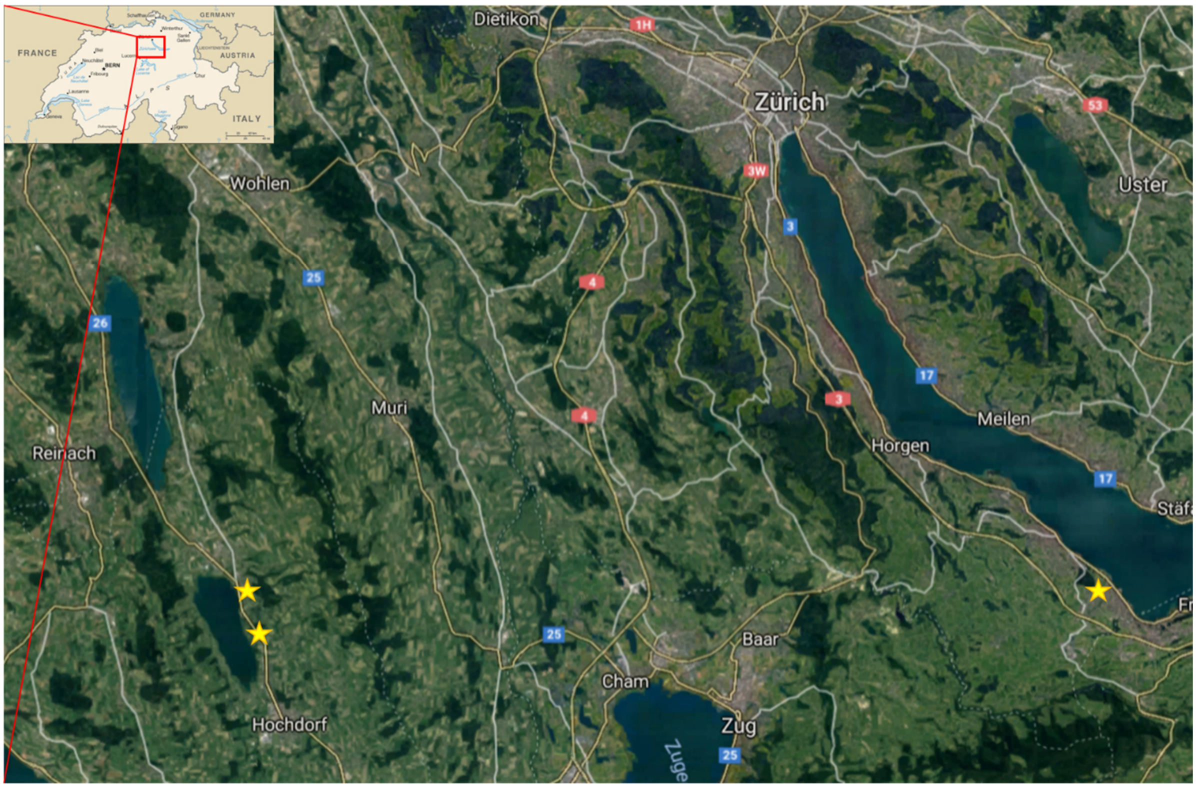

Figure S1: Location of the three study orchards (yellow stars) in Switzerland: Kleinwangen (lower left), Gelfingen (upper left), Waedenswil (right).

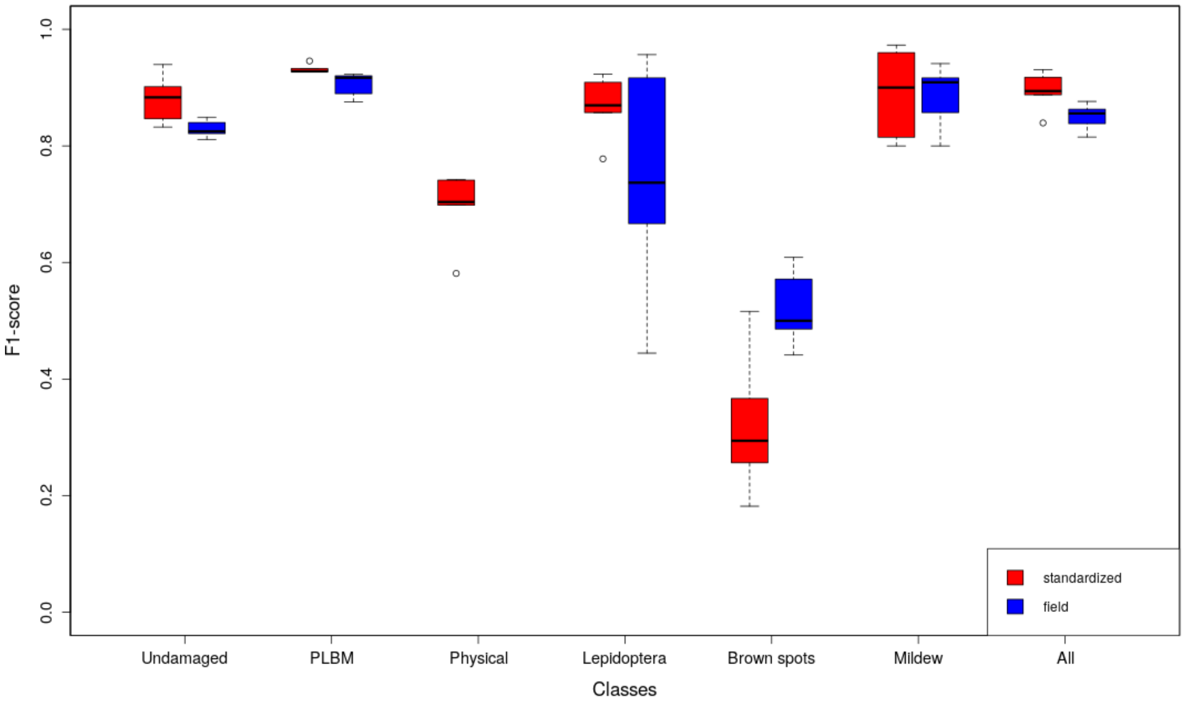

Figure S2: DNN performance for the 14 classification tasks measured as F1-scores. Boxes show the classification accuracy variation over the 5-fold cross validation. Red boxes show the results for standardized pictures, blue boxes for field pictures.

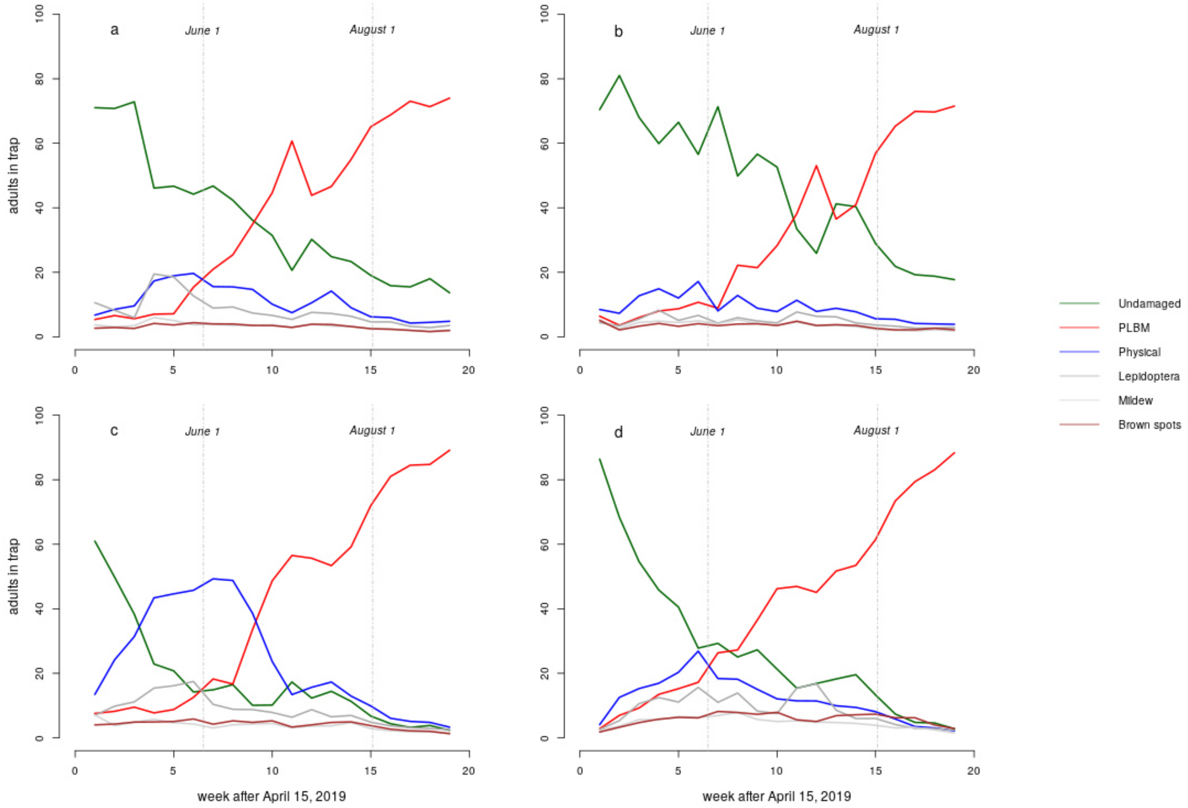

Figure S3: Reconstruction of the phenology for all damage classes for Gelfingen standardized pictures (a), Gelfingen field pictures (b), Kleinwangen standardized (c) and Kleinwangen field (d).

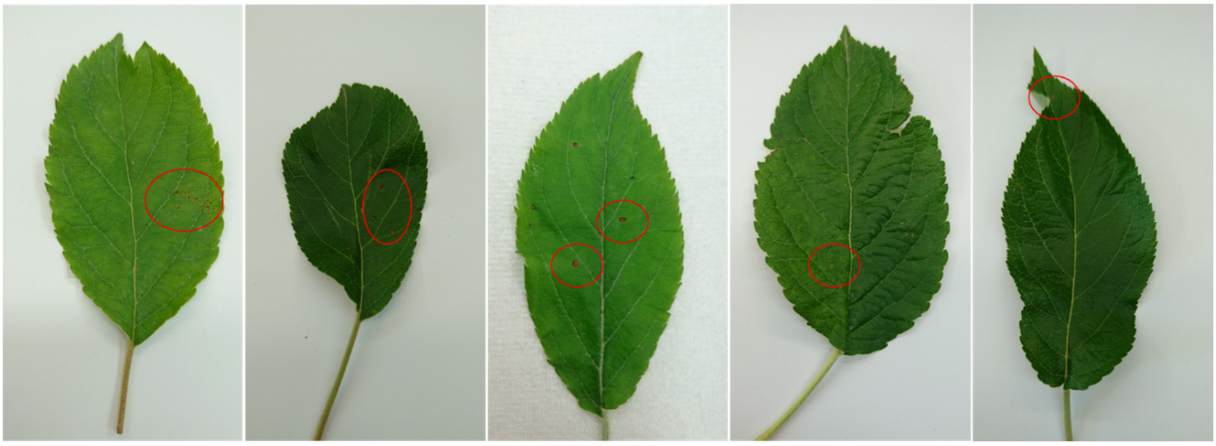

Figure S4: Examples of wrongly classified standardized pictures. F.l.t.r.: *Physical damage* instead of *Brownspots*; *PLBM* instead of *Brownspots*; *PLBM* instead of *Brownspots*; *PLBM* instead of *Physical damage*; *Undamaged* instead of *PLBM*.

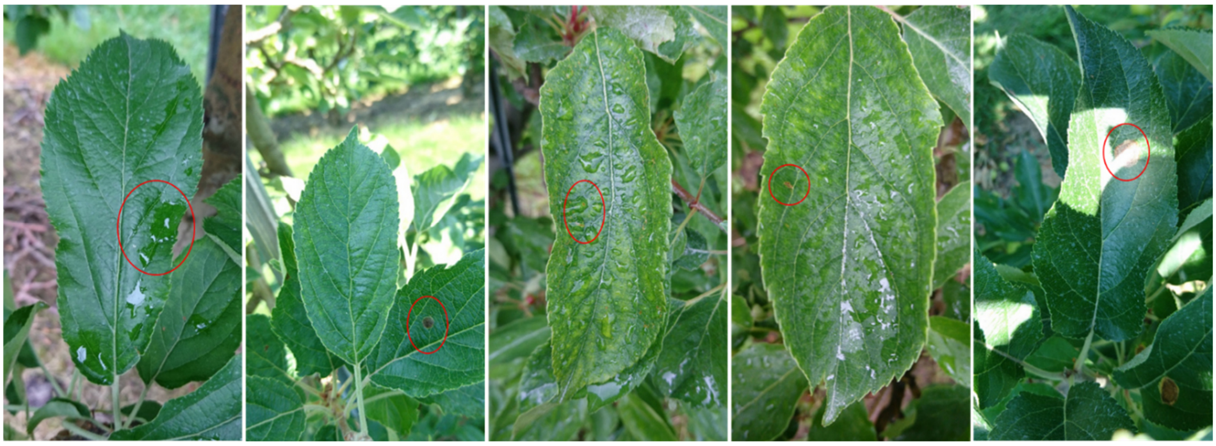

Figure S5: Examples of wrongly classified field pictures. F.l.t.r.: *PLBM* instead of *Undamaged*; *PLBM* instead of *Undamaged*; *Undamaged* instead of *Brownspots*; *Undamaged* instead of *Physical damage*; *Undamaged* instead of *PLBM*.

CONCLUSION AND PERSPECTIVES

The motivation for this thesis was to provide better understanding on how the distribution of insect pest species will be affected by future climate change. In particular, using spatial modelling approaches, this thesis contributes to a better understanding of: (i) the impact of climate change on insect pest pressure, (ii) the consistency between inductive and deductive modelling approaches for pest distribution modelling, (iii) how the structure of pest – host plant metawebs will change in the near future, and (iv) implications of future insect pest occurrence for plant protection services. Furthermore, using deep neural networks, this thesis also investigates (v) how novel technologies may bring new opportunities to pest damage forecasting.

The impact of climate change on insect pest pressure

This thesis contributes to a better understanding of spatial and temporal dynamics of climatic suitability for insect pest species in Europe under climate change (*Chapter 1* and *Chapter 2*). As defined in *Chapter 1*, pest pressure is quantified here as the number of species with suitable climatic conditions in a region. In *Chapter 1,* I show that the majority of 89 quarantine (i.e. black-listed) pest species, which have not yet established in Europe, encounter suitable conditions in southern Europe under current climate, underlining high current-day pest pressure in these regions. With progressing climate change, the suitable climate conditions of insect pest species shift towards higher latitudes (Bebber et al., 2013), thus imposing increasing pest pressure on European agriculture and forestry. *Chapter 2* confirms this trend with two comprehensive sets of insect pest species, including established pests and quarantine pests that were previously considered mainly in isolation. The combination of two methodological approaches (inductive and deductive), to compare fundamental and realized climatic niches, further supports the findings of higher pest climatic suitability in temperate regions (Yan et al., 2017) and increasing pest pressure on plant production systems under climate change (Deutsch et al., 2018). Further, I corroborate the results of earlier studies that showed expanding potential distribution for individual insect pest species across Europe (e.g. for *Popilia japonica*; Kistner-Thomas, 2019) by investigating their climatic suitability as component of the comprehensive lists of insect pest species included in *Chapter 1* and *Chapter 2.* Finally, I find that western and central Europe will be threatened by increasing pest pressure in the near future, and also northern and eastern Europe will face higher pest pressure towards the end of the current century.

Determining inflection points in pest niche accumulation is valuable to anticipate non-linear changes in pest pressure under climate change. However, to the best of my knowledge, studies investigating non-linearity of pest pressure are missing so far. *Chapter 2* identifies an inflection point around -3°C minimum temperature of the coldest month, beyond which the number of pest species encountering suitable climatic conditions will drastically increase, promoting a rapid enhancement of pest pressure. This inflection point marks a transition between the groups of cold-adapted and warm-adapted pest species. Once this threshold is crossed, warm-adapted pests that are not going through a winter diapause will find increasingly suitable conditions. Therefore, under climate change, regions that cross this inflection point temperature are threatened by an acceleration in pest invasions. The choice to use a minimum temperature gradient to investigate niche distribution in climatic space is well justified, because minimum temperature is the main limiting factor for species distribution in colder regions, therefore also preventing from new pest invasions (Maxmen, 2013; Jarošik et al. 2015).

Comparison of inductive and deductive distribution models

Hutchinson's niche concept distinguishes between the fundamental and the realized niche of species (Hutchinson, 1957). While the fundamental niche defines the distribution of a species based on abiotic environmental limits, the realized niche is additionally restricted by biotic effects, such as competition or predation (Hutchinson, 1957; Wiens et al., 2009; Soberón & Arroyo-Peña, 2017). *Chapter 2* uses species distribution models (SDMs) to map the realized niche (Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005; Elith & Leathwick, 2009) and physiological models to map the fundamental niche (Kearney & Porter, 2009; Venette et al., 2010), giving two alternative perspectives on the potential distribution of established and quarantine pest species. Although conceptual differences of the two modelling approaches (Venette et al., 2010; Tonnang et al., 2017) are observable from species level comparisons, where projections differ widely in some cases, at a broader assemblage scale results from these different approaches tend to agree and predict an increasing pest pressure across Europe. The benefit of combining approaches is that if models agree, their predictions are expected to be more robust, while model disagreement can foster new insights and hypothesis (Hijmans & Graham 2006). Specifically, we find model disagreements whereby the realized niche is narrower than the fundamental niche (*Chapter 2*; Soberón & Arroyo-Peña, 2017). As a result, there is less restriction from spatial predictions of physiological models at southern range boarders, leading to differences in predicted species communities in southern Europe. However, the broad scale increasing climate suitability for pest species towards higher latitudes is congruent across models, adding additional robustness to the results from *Chapter 1*.

Looking at the similarities and discrepancies between fundamental and realized niches is particularly interesting for species shifting their distribution range or invading new regions (Tingley et al., 2014). This can foster insights on the invasion process, such as realized niche shifts (Tingley et al., 2014), because those species are not at equilibrium with the environment (Hill & Thomson, 2015). The realized niche in the invasive range of a species may differ from the realized niche in the native range, because biotic constraints, such as competition or predation, are absent (Broennimann et al., 2007). This allows the species to express another part of its fundamental niche (Broennimann et al, 2007; Alexander and Edwards, 2010). Shifts in the realized niche can also be caused by intraspecific variation in niche requirements, meaning that a population in the invasive range may tolerate a different set of climatic conditions than the population in the native range because the invasive population was drawn from a specific area of the native range (Peterson & Holt, 2003; Strubbe et al., 2013). Meanwhile, the fundamental niche does not change unless there is evolutionary or epigenetic change (Müller-Schärer et al., 2004, Broennimann et al., 2007). Together, investigating the fundamental niches using process-based models can give valuable insights on the potential species distribution in the invasive range (Kearney et al., 2008), while investigating the realized niches using SDMs is useful to anticipate the area of introduction and establishment of non-native species (Broennimann et al., 2007). Pest pressure on European agriculture is increasing under climate change, however, host availability (Niemelä & Matteson, 1996) and propagule pressure (Lockwood et al., 2005) are also crucial drivers of invasion success (Bacon et al., 2014).

The impact of climate change on pest – host linkage and suitability overlap

Host availability is crucial for pest establishment and invasion (Niemelä & Matteson, 1996; Bacon et al., 2014). The changes in the linkage and the spatial overlap between insect pests and their host plants under climate change inform on potential host availability for pest species and therefore on regions at elevated invasion risk. Metawebs, or interaction network approaches have been applied to ecological problems in natural ecosystems to investigate network structures and impacts of climate change on species interactions and food webs (Dunne, 2006; Pellissier et al., 2018). For instance, metaweb approaches based on species distribution models have informed on changes in food web structures of fish species under climate change (Albouy et al., 2014). While ecological network approaches can inform on interactions in agricultural systems (e.g. Saunders & Rader, 2019) previous work has, to the best of my knowledge, not quantified changing pest-host interactions under climate change. *Chapter 1* adopts such an ecological network approach to investigate the impact of climate change on linkage and suitability overlap between insect pests and their host plants, delivering new insights on general trends of pest-host interactions under climate change. Potential interactions based on published host lists for each pest species are used to investigate the realized linkage as modelled distribution overlap in Europe. Although the structure of the metaweb is relatively simple, it creates valuable insights on the effects of climate change on pest-host interactions and allows a more integrative understanding of the network system (Pellissier et al., 2018), and therefore on pest pressure and invasion risk in different regions under climate change.

Host availability for insect pests is dynamic and expected to change under climate change, as the distribution of managed plants depends on climatic factors similarly as unmanaged plants (Connor, Loomis & Cassman, 2011). To adequately inform on host availability under climate change, I therefore use SDMs to investigate how crop and forest tree distribution will change in the future (*Chapter 1*). This creates new insights on large-scale patterns of crop and forest suitability across Europe. I investigate the climatic suitability of 96 crops and 30 forest tree species, therefore allowing inference on trends of host plant suitability change rather than how the distribution of single plant species is affected by climate change (e.g. maize, Ramirez-Cabral, Kumar & Shabani, 2017). While in southern Europe the climatic suitability for crops and forest trees decreases until the end of the century, those plants will generally find increasing climatic suitability in central, eastern and northern Europe. This will open up new opportunities for cultivation (Maracchi, Sirotenko, & Bindi, 2005) without increasing cropping areas. These results indicate that growers in large parts of Europe may benefit from the cultivation of more valuable crops as they find increasingly suitable climatic conditions, for instance wine production in northern Europe (Bindi et al., 2001). In addition, diversification is often assumed to boost the resilience of cropping systems against disturbances (Lin, 2011). However, the capitalization of these opportunities may be hampered by increasing pest pressure associated to the new crop species. With larger scopes of different crops, host availability increases for pests, promoting establishment and spread, and therefore putting more pest pressure on the presently grown crops.

The analysis of the area of overlap between pests and their host plants is particularly relevant because invasion success of pest species depends on host availability (Niemelä & Matteson, 1996; Bacon et al., 2014). The metaweb approach combines two main drivers of insect pest invasions, host availability and climatic suitability (Ward & Masters, 2007; Bacon et al. 2014). The results of the metaweb approach show highest linkage and overlap in southern Europe, which will slightly decrease by the end of the century, as climate conditions for both, pests and plants will become increasingly unsuitable in southern Europe (Bindi & Olesen, 2011). Northern Europe is currently less threatened by pest invasions, but with increasing crop suitability, more pest species could not only encounter suitable climate conditions but also available host plants. Investigating the metaweb structure further shows that specialisation decreases and more links per pest species become realizable. Particularly polyphagous pests will benefit from climate change because their potential distribution overlaps with many host plants. This confirms that generalist species pose the greatest risk of invasion, as those species are most likely to encounter host plants in newly occupied areas (Ward & Masters, 2007). Increasing pest pressure because of warming climate in Europe will thus be intensified by a growing area of overlap between pests and their host plants because climate suitability of crops and forest trees will also be affected by climate change. *Chapter 1* shows that the increasing linkage and climatic suitability overlap between pests and their host plants additionally favours pest invasions across Europe, posing new challenges to plant protection in the near future.

Implications from increasing pest pressure for plant protection

Border control and surveillance measures are crucial to prevent introduction of insect pests (Bacon et al., 2012). Strong efforts by plant protection services will be required to minimize the risks associated to invasive insect pests, as climate change increases the invasion risk (i.e., *Chapter 1* and *Chapter 2*) and global trade and travel support the transport of insect pests (Hulme et al., 2009; Liebhold et al., 2006; Roques, 2010). While I demonstrate that climatic suitability and host availability for insect pest species are strongly increasing in the future due to warming climate, propagule pressure largely depends on global trade and travel (Liebhold et al., 2006; Hulme, 2009; Roques et al., 2010; Bacon et al., 2012). Global traffic is expected to further increase in the near future (Levine & D'Antonio, 2003; Sardain, Sardain &

Leung, 2019). Meanwhile, the pool of invasive species seems to be insatiable (Seebens et al., 2017), and continuously more regions are connected to the global trade market, serving as newly accessible pools for potentially invasive species (Seebens et al., 2018). Currently, large regions of the Mediterranean already provide suitable climate conditions for the majority of quarantine pests and their host plants (*Chapter 1* and *Chapter 2*). This thesis identifies these regions as potential entry gates for pest invasions, as non-native pests establish and spread from there as climate warms, as for example *Tuta absoluta* (Desneux et al. 2010). Indeed, those regions exhibit the highest numbers of established non-native invertebrate species (Roques et al., 2009). Furthermore, I identify a threshold releasing pests from abiotic constraints allowing spread from the initial entry gates, for example, when rising temperatures in central Europe cross a threshold in minimum temperatures of the coldest month around -3°C, obtained from the results of *Chapter 2* (i.e. inflection point temperature). Crossing this inflection point temperature enables the spread of non-native pests from the entry gates to new areas. Therefore, the results of *Chapter 1* and *Chapter 2* urge for strong efforts from plant protection services, as decreasing propagule pressure is crucial to prevent invasions and will become even more important under climate change (Bacon et al., 2012; Bacon et al., 2014). Although different sampling strategies have been proposed to optimize inspections of plant material, capacities are limited (Bacon et al., 2012; Chen et al, 2018) and only a small fraction of the trade goods are inspected (McCullough et al., 2006; Poland & Rassati, 2019). To support the plant protection services to more efficiently anticipate invasion of new pest species and prepare management strategies, providing data on their current and potential future distribution serves as valuable contribution.

A way to support plant protection services in conducting pest risk assessments is to generate forecasts of the potential distribution of pest species by providing pest risk maps (Venette et al., 2010). The findings of *Chapter 1* and *Chapter 2* underline the importance of plant protection services for effective inspection of trade goods and prevention from pest invasions. Hence, the results emphasize strongly that efforts from all stakeholders are needed and that European plant health depends on the collaboration of all member states (MacLeod et al., 2010) to minimize the costs associated to insect pest invasions. Information on potential distribution contributes to pest risk assessments (Venette et al., 2010) for individual species, helping to categorise and decide whether pests ought to be prioritized as quarantine pests (Baker et al., 2009; EFSA Panel on Plant Health, 2018). Once potential locations for establishment of a species are identified, targeted monitoring can be conducted, for instance with DNA based tools (Darling & Blum, 2007), remote sensing (Rocchini et al., 2015), pheromone or kairomone trapping (Poland & Rassati, 2019) or sentinel host plants (Kenis et al., 2018). The results of this thesis can therefore be used for pest risk mapping and planning of monitoring actions. In light of the increasing globalisation, even with stronger plant health regulations, more efficient border surveillance and stronger efforts for pest monitoring, new species must be expected to invade parts of Europe (Bacon et al., 2014). Therefore, strategies have to be developed to deal with higher pest pressure and new tools for seasonal pest forecasting may help to absorb some of the impacts of those invasive species.

Novel opportunities for pest forecasting

With increasing pest pressure challenging sustainable plant protection under climate change, the demand for new tools for plant protection increases and big data and deep learning open new opportunities to meet those demands and support pest management. Big data brings many new opportunities to agriculture (Kamilaris et al., 2017; Coble et al., 2018), including pest forecasting, as data-driven approaches can be used to create robust relationships between pest occurrence and meteorological data (Orlandini et al. 2020). For instance, such data-driven approaches may help to overcome current limitations of phenology models, such as labour- and cost-intensive development and increasing discrepancies between model predictions and field observations due to disruption of pest and host phenology under climate change (Kingsolver et al., 2011). Although deep neural networks and big data have been used for pathogen and pest classification (e.g. Mohanty et al., 2016, Cheng et al., 2017), to my knowledge these technologies have never been applied in a pest forecasting context. *Chapter 3* presents a novel approach for a forecasting model as part of a proposed framework for the development of decision support systems. In particular, the proposed framework connects data collection to create big data sets with deep neural networks to produce phenological models for pest damages. The results of *Chapter 3* show that deep neural networks are capable of classifying pest damages recorded with smartphone pictures and that the phenology of pest damages can be obtained from a big dataset using a classification model established with deep neural networks. Coupled with meteorological variables, the phenology can then be used to construct a phenological model. More precisely, the case study presented in *Chapter 3* highlights that this approach is applicable to model the phenology of mines produced by larvae of the pear leaf blister moth (*Leucoptera malifoliella,* Costa) on apple leaves. The established deep neural networks perform well for different classes of damages individually and in multiclass approaches. Performance is better on classes with many images available for training, and models trained with pictures taken under standardized conditions perform better than those trained with pictures taken in the field. Compared to studies using deep neural networks to classify plant pathogens from leaf pictures, the performance of the networks presented in *Chapter 3* are slightly lower (Barbedo, 2018). However, earlier studies concentrated on the classification tools alone and used full datasets for training and evaluation (e.g. Mohanty et al., 2016). Meanwhile, *Chapter 3* used only a small proportion of the images for model training. The remaining images were used to test whether phenologies can be reconstructed. Still, the results of this case study underline that pest forecasting could benefit greatly from exploiting modern technologies for data collection (e.g. with drones; Finn and Donovan, 2016) and data analysis (i.e. deep neural networks; Goodfellow et al., 2016), provided adequate data availability. In the context of the framework for developing novel decision support systems, big data and deep neural networks provide powerful tools, although new methods for data collection must be established first.

Collectively, the three chapters presented show that the pest pressure from established and quarantine insect pest species is increasing in Europe under climate change. I use two complementary modelling approaches to provide additional robustness to the predictions of pest climatic suitability and obtain an inflection point temperature beyond which the number of species encountering suitable climate will drastically increase. In addition, I address host availability as crucial factor for insect pest invasion using a metaweb approach and show that linkage and suitability overlap between insect pests and their host plants must be expected to increase in Europe under climate change. Finally, I show that big data and deep neural networks could support developing data-driven pest forecasting models.

Perspectives

Pest risk analysis

The impact of invasive insect pests on global crop yields is increasingly considered as one of the main challenges for food security (Oerke, 2006; Bradshaw et al., 2016; Deutsch et al., 2018). This thesis provides a better understanding of the spatial and temporal patterns of pest pressure for Europe under climate change and shows that increasing host availability elevates the risk of invasion by insect pests. These findings are particularly valuable for decision-makers in the plant protection sector and suggest action, such as dissemination of the current knowledge and raising the awareness of this challenge. Insights on which quarantine species pose risks to certain areas may help to better prepare for pest invasions and gain time to implement management strategies, such as prevention, early detection and eradication, containment and various forms of mitigation (Pyšek and Richardson, 2010). However, C*hapter 1* and *Chapter 2* would have benefited from the availability of more occurrence data and data on physiological thresholds of pest species. For many quarantine species, no or little data were available. With improving data availability, the set of pest species may become even more representative as distribution models for additional species could be established. Additionally, better computational power and climate data quality will help to produce predictions with higher temporal and spatial resolution, allowing to extract even more valuable information from such models.

Developing new tools that meet specific needs of pest risk analysts would improve the support to plant protection services. Although, species distribution models and physiological models can be directly used for basic pest risk mapping (Venette et al., 2010), other factors, such as spread (Robinet et al., 2012) or economic impact (Soliman et al., 2010) need to be addressed in pest risk analyses. Coupling those factors directly to pest distribution models could be of great value for plant protection services. For instance, combining pest distribution models with more sophisticated process-based crop models instead of crop distribution model as in *Chapter 1*. Yield and productivity forecasts under climate change depend on complex interactions between several mechanisms and process-based crop models can for instance include beneficial effects from CO_2 fertilization (Challinor et al., 2014) or detailed information on irrigation regimes that might change in the future depending on water availability (Elliot et al., 2014). Therefore, combining sophisticated crop models with pest distribution models would allow to focus on the economically most relevant pest species threatening crop productivity under climate change.

Pest damage forecasting

This thesis further shows that development of new pest forecasting models relying on big data and deep neural networks is feasible, although future work needs to address the current lack of data availability. Open image datasets in the agricultural domain are scarce, particularly on pest and pathogen damages, therefore slowing down advances in pest and pathogen classification (Barbado, 2018; Kamilaris & Prenafeta-Bolú, 2018). To develop decision support systems based on big data and deep neural networks for broader application, new approaches for data collection must be established first. *Chapter 3* suggests two different approaches to tackle this challenge. On the one hand, the implementation of drones is a matter of financial resources, as high-tech cameras and drones are expensive, although this would be a one-time investment that can be shared by grower communities. On the other hand, the citizen science approach requires the initial investment for network establishment, which may pay off in the longer term as additional beneficial effects may arise from including farmers in the development (Lynch, Gregor and Midmore, 2000). Indeed, one of the main challenges for the implementation of a decision support system is convincing growers to actually use it. Nevertheless, in an unrepresentative survey I conducted during *Chapter 3*, growers showed interest in such new tools. In addition, citizen science could help to detect invasive species (Hulbert et al. 2017), as famers will be specifically interested in categorizing unknown damages.

The development of robust and efficient pest forecasting tools could imply opportunities for the management of invasive pest species. As pest pressure and invasion risk are expected to increase under climate change, the implementation of novel technologies to support sustainable intensification gains in relevance. The major advantage of the effective implementation strategy of pest forecasting shown in *Chapter 3* is that such tools can be quickly adapted to new pest species. However, applying phenological models for decision support needs additional efforts. To provide recommendations on management interventions and their optimal timing, solid testing of plant protection measures is crucial. Nevertheless, the proposed approach for pest forecasting presents a fast and efficient strategy to model pest damage phenology, which is particularly useful in the situation where an increasing number of newly occurring pests is expected. Finally, my hope is that the proposed framework approach can be used location independent, meaning that countries lacking in resources and knowledge on pest and disease management could benefit greatly from such tools.

This thesis shows that different modelling approaches are useful tools for several applications in plant protection and pest management. Spatial modelling can provide valuable information on the potential distribution of insect pests and could become even more useful for pest risk analysts by including additional important factors that inform on the potentially most relevant pest species. Although the need for development of new approaches for pest damage forecasting is growing independently from increasing pest pressure under climate change, the significance of perspectives arising from modern technologies to support sustainable food production cannot be overemphasized.

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